The application of modern statistical approaches to identify consistent individual differences in the behaviour of wild postpartum female grey seals (Halichoerus grypus)

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The application of modern statistical approaches to identify consistent individual differences in the behaviour of wild postpartum female grey seals (*Halichoerus grypus*)

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Abstract

Consistent individual differences (CIDs) in behaviour have been shown to occur in a large number of species. However, few studies have attempted to quantify CIDs in the behaviour of wild animals in their natural environment. Yet, in order to understand the ecological and evolutionary relevance of CIDs in behaviour, it is fundamentally important that we attempt to quantify them in wild animals, *in situ*.

In order to address this question, a three-step analytical approach was applied to data that were collected on wild postpartum female grey seals, which were part of a 'hands-off' observational study. Aspects of behaviour were highly repeatable across breeding seasons. The 'alert' behaviour in particular, remained highly repeatable irrespective of which individuals were included in the analyses. Furthermore, these robust repeatability estimates for the 'alert' behaviour persisted, despite controlling for social and environmental factors that are known to influence maternal behaviour.

Subsequently, the three-step analytical approach was applied to an independent dataset collected on postpartum female grey seals that are part of a long-term longitudinal study on reproductive variation. Similar patterns were observed in the results across the three steps, and once again, the 'alert' behaviour was one of the more repeatable behaviours. However, these highly repeatable behaviours did not explain any of the variation in commonly used proxies for short-term fitness. As a result, these preliminary findings add to the debate on whether or not CIDs in behaviour are adaptive or are a product of phenotypic and/or genotypic constraints. Consequently, the potential influence of CIDs in behaviour on fitness trade-offs, population dynamics and conservation and management practices shall be discussed.

The application of the three-step analytical approach to the independent dataset did raise some important methodological considerations, which shall be discussed in relation to developing guidelines for applying this approach to other datasets.

Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported here has been conducted by the author unless stated otherwise.

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Chapter One:
Individual variation and its potential ecological and evolutionary relevance

1.1. Introduction

Since its publication in 1859, the theory of natural selection has been used to explain the mechanism driving differences between: 1) genera and higher-level taxa, 2) closely related species and subspecies, and 3) populations of the same species (Darwin, 1859; Dall et al., 2004; Wolf & McNamara, 2012). In contrast, despite a few well-known forms of adaptive individual variation (e.g. polymorphisms in mimicry (Mallet, 1999) and male colour polymorphism (Olsson et al., 2007; Gray et al., 2008)), differences within a single population were traditionally regarded as non-adaptive noise that did not call for a deeper explanation (Wilson, 1998; Dall et al., 2004; Wolf & McNamara, 2012). However, in the last decade, this view has changed substantially due to an exponential growth in the number of studies which have shown that individuals within populations do differ consistently in a broad range of behavioural traits, such as aggressiveness (Huntingford, 1976; Johnson & Sin, 2005), activity (Mather & Anderson, 1993; Carere et al., 2005), exploration (Dingemanse et al., 2004), risk-taking (Wilson et al., 1993; Coleman & Wilson, 1998) and sociability (Cote et al., 2008). These consistent individual differences (CIDs) in behaviour have been shown to occur across a broad range of ecological conditions (e.g. different levels of predation risk) and behavioural contexts (e.g. feeding, mating and parental care). Furthermore, these CIDs in behaviour have also been recorded across a broad range of taxa, from cnidarians (Briffa & Greenway, 2011) to mammals (Martin & Réale, 2008a). Consequently, there has been much debate on whether consistency in an individual's behaviour is adaptive or is a product of phenotypic and/or genotypic constraints (e.g. DeWitt et al., 1998; Dall, 2004; Dingemanse & Réale, 2005).

1.2. Quantifying CIDs in behaviour

The majority of studies investigating CIDs in behaviour use specific behavioural tests to assess whether or not a group of individuals can be defined

by a particular 'behavioural axis' (e.g. Drent et al., 2003; Bell, 2005; Réale, et al., 2007; Smith & Blumstein 2008). There are five behavioural axes as defined by Réale et al. (2007; Table 1.1), and of these the 'shyness-boldness', which is defined as an individual's reaction to a risky but not novel situation (Wilson et al., 1994) is the more commonly tested. To quantify the shyness-boldness behavioural axis the latency of an individual to emerge from a refuge and/or feed after a simulated predator risk is measured (e.g. Huntingford, 1976; Bell, 2005; Wilson & Stevens, 2005; Alvarez & Bell, 2007; Wilson & Godin, 2009). If an individual consistently takes longer to emerge from their refuge (and/or feed) then they are classified towards the 'shy' end of the axis. Conversely, if an individual takes consistently less time to emerge (and/or feed) then they are classified towards the 'bold' end of the axis (Figure 1.1). There are also a number of empirical examples for the 'exploration-avoidance' (e.g. Dingemanse et al., 2004; Dingemanse et al., 2007), 'activity' (e.g. Sih et al., 2003; Boon et al., 2008), 'aggressiveness' (e.g. Huntingford, 1982) and 'sociability' (e.g. Muller & Schrader, 2005; van Oers et al., 2005a) behavioural axes. These shall not be discussed here; however, the general experimental frameworks that are commonly used to address each of these can be found in Table 1.1.

Table 1.1: The behavioural axes that are commonly used to study CIDs in behaviour, as defined by Réale et al. (2007).

Behavioural axis	**The behavioural measure for each individual**
Shyness-boldness	Reaction to a risky but not novel situation
Exploration-avoidance	Reaction to a novel situation
Activity	Level of activity
Aggressiveness	Aggressive behaviour to a conspecific
Sociability	Reaction to the presence and/or absence of conspecifics

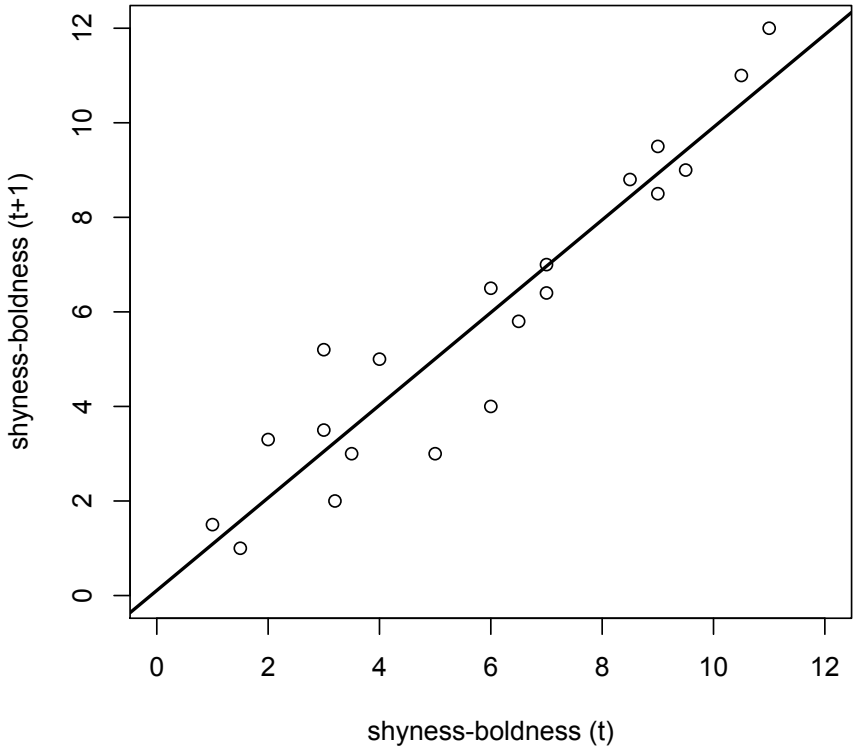


Figure 1.1: An example of consistent individual differences in the shyness-boldness behavioural axis across two different points in time (t and t+1), each data point represents an individual and the black line shows the 1:1 line. Individuals with low values are regarded as 'shy', and conversely, individuals with high values are regarded as 'bold'.

1.3. A difference of opinion: the definitions and terms used

The interest in CIDs in behaviour has grown rapidly over recent years (Figure 1.2; Réale et al., 2010), which has lead to numerous and often conflicting (or at best subtly different) combinations of definitions and terms used in this field of evolutionary and behavioural ecology (e.g. Sih et al., 2004; Réale et al., 2007; Sih & Bell, 2008; Dingemanse et al., 2010; Stamps & Groothuis, 2010a; Uher, 2011). Throughout the literature, the most commonly used terms are 'personality', 'temperament', 'coping styles' and 'behavioural syndromes' (Sih et al., 2004; Groothuis & Carere, 2005; Réale et al., 2007; Stamps & Groothuis, 2010a, b). In many studies these terms have been regarded as analogous, and are typically defined as "between-individual consistency in behaviour, which occurs across two or more contexts **and/or** time points" (Sih et al., 2004; Bell, 2007; Wolf et al., 2007;

Sih & Bell, 2008, pp 231 - 232. However, see Stamps & Groothuis, 2010a for alternative definitions of these terms). For the purpose of this chapter, these terms and definitions are considered synonymous, and shall be referred to as CIDs in behaviour. Therefore, CIDs in behaviour can occur in:

1) The same context but at different points in time (e.g. aggression in a social context at three different points in time; D'eath, 2004; e.g. Figure 1.1).
2) Different contexts at the same point in time (e.g. aggression towards a mate versus aggression towards prey; Johnson & Sih, 2005).
3) Different contexts at different points in time (e.g. aggression towards conspecifics versus boldness under predation risk; Bell & Sih, 2007).

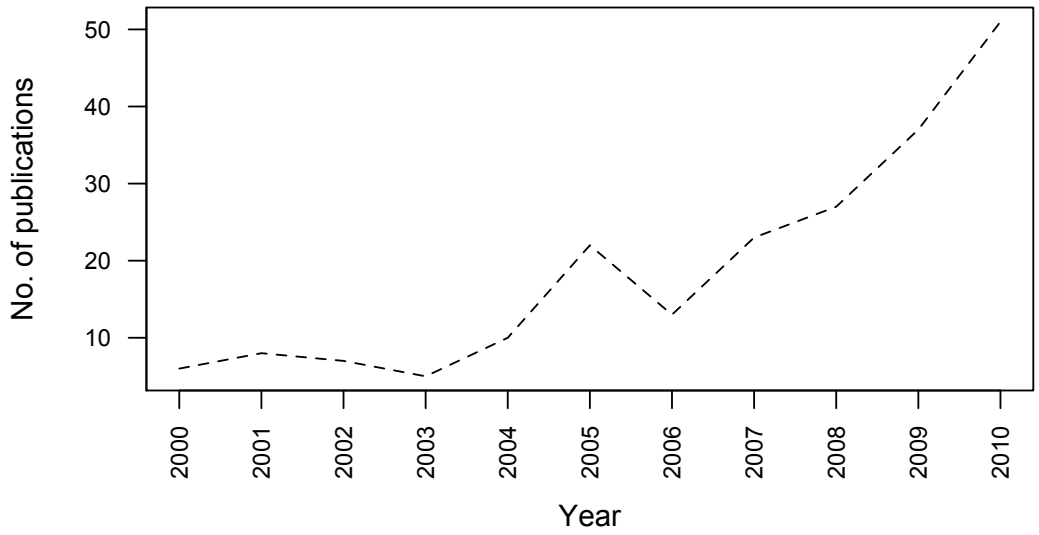


Figure 1.2: The number of articles published on the consistency of individuals' behaviour in the journals: Animal Behaviour, Behaviour, Behavioural Ecology, Behavioural Ecology and Sociobiology, Biology Letters, Journal of Animal Ecology, and Proceedings of the Royal Society B between 2000 and 2010. The terms used in a Web of Knowledge search of these journals were: 'personality', 'behavioural type', 'behavioural syndrome', 'consistent individual differences' and 'repeatability' (synonymous with consistency). Only publications on repeatability of individuals (not groups and/or populations) were included, and all studies on humans and all review articles were omitted. Consequently, the total number of articles published on this topic in the aforementioned journals between 2000 and 2010 was 214.

1.4. An adaptive conundrum: how can CIDs in behaviour be maintained in a population?

Traditionally, behaviour was considered to be highly plastic, such that all individuals were capable of exhibiting the optimal behaviour in a given situation and/or context (Dall et al., 2004; Sih et al., 2004; Bell, 2007). However, by definition, individuals that behave consistently must be limited to some degree in their behavioural plasticity. This may, in the first instance, appear to be somewhat maladaptive; however, there are potential costs and limitations to maintaining plasticity that could explain why consistency in an individuals' behaviour may occur. These include, but are not limited to, 'lag-time limits': where the time taken to respond to environmental change results in a maladaptive phenotype; 'information reliability limits': if individuals are 'wrong' about the environment then this may result in a maladaptive phenotype; 'acquisition and maintenance costs': acquiring information and maintaining the sensory and regulatory mechanisms that produce plasticity could be too costly to maintain in a rapidly changing environment (DeWitt et al., 1998). Consequently, it may be more beneficial for individuals to use an intermediate approach that would allow the individual to balance the trade-offs between the higher costs associated with optimal behavioural plasticity and the lower costs of a more fixed approach (DeWitt, 1998; DeWitt et al., 1998). Therefore, the consistency of behaviour expressed by individuals may represent this trade-off.

There is theoretical and empirical support for CIDs in behaviour being maintained by life-history trade-offs (e.g. Stamps, 2007; Wolf et al., 2007; Biro & Stamps, 2008; Smith & Blumstein, 2008; Réale et al., 2009). Stamps (2007) and Biro & Stamps (2008) suggest that behavioural patterns that increase both growth and mortality rates (e.g. foraging under predation risk) would be positively correlated with one another across individuals. Consequently, selection for high growth rates will increase mean levels of potentially risky behaviour across populations, and that within populations, faster growing individuals will take more risks in foraging contexts than slower growing individuals. Using a similar framework, Biro & Stamps (2008) also consider a life-history trade-off between fecundity and mortality. They support both hypotheses by citing several studies,

which have shown that CIDs in activity or activity and boldness were positively related to growth or fecundity, and negatively related to survivorship in the presence of predators, or negatively related to longevity in the absence of predators (see references therein). Furthermore, a meta-analysis of studies reporting fitness consequences of CIDs found that bolder individuals had increased reproductive success, but incurred a survival cost, thus supporting the hypothesis that variation in boldness is maintained by a trade-off in fitness consequences across contexts (Smith & Blumstein, 2008). If the fitness associated with these CIDs in behaviour is frequency dependent, then this could lead to the stable coexistence of different behavioural 'types' within populations (Maynard Smith, 1982; Dall et al., 2004; Wolf et al., 2007; Carere et al., 2010; Wolf & Weissing, 2010). However, in order for frequency dependence to maintain CIDs in behaviour, fixed proportions of individuals would have to maintain their 'behavioural type', consistently (Dall et al., 2004).

Spatial and temporal environmental heterogeneity has also been shown to maintain diversity between individuals (Kassen, 2002; Carere et al., 2010; Wolf & Weissing, 2010), which suggests that certain types of individuals may be more successful under different environmental situations and/or contexts than others (Dingemanse et al., 2003; Sih et al., 2003; Dingemanse et al., 2004). This may also be reflected in a number of studies, which have shown that certain environmental parameters do influence selection and reproductive success (e.g. Réale et al., 2003; Huntingford & Adams, 2005; Nussey et al., 2005a, b; Spottiswoode et al., 2006; Twiss et al., 2007). There is also evidence that environmental factors during ontogeny do influence individual variation in behaviour (Carere et al., 2005; Groothuis & Carere, 2005; Nussey et al., 2007b); however, there has been little research to-date, which has attempted to quantify the developmental processes resulting in CIDs in behaviour (Sinn et al., 2008b; Dingemanse et al., 2009; Stamps & Groothuis, 2010a, b and Groothuis & Trillmich 2011; Trillmich & Hudson, 2011).

Irrespective of how CIDs in behaviour arise or are maintained, the resulting limitations on behavioural plasticity are likely to affect an individual's fitness in a given environment and under varying environmental conditions. For example,

some studies have shown that more aggressive individuals are less behaviourally flexible than others when experiencing environmental change (Ellenburg et al., 2009). There is also evidence from trapping studies that more active individuals are more likely to be caught (Boon et al., 2008). More specifically, there are a growing number of studies that have found correlations between CIDs in behaviour and physiological factors (Carere et al., 2003; Anestis, 2005), body size (Brown et al., 2005), dispersal (Dingemanse et al., 2003; Martin & Réale, 2008b), recruitment (Armitage, 1986), survival (Réale & Festa-Bianchet, 2003; Sinn et al., 2008a), and reproductive success (Johnson & Sih, 2005). Furthermore, some of these studies have provided evidence of a genetic basis to CIDs in behaviour (Réale & Festa-Bianchet, 2000; Dingemanse et al., 2002; Drent et al., 2003; van Oers et al., 2004; Bell, 2005; Groothuis & Carere, 2005; Sinn et al., 2006; Pelletier et al., 2007; Dingemanse et al., 2009), which suggests that there maybe genetic costs to behaviour plasticity, such as linkage, pleiotropy and/or epistasis (DeWitt et al., 1998; Bell & Aubin-Horth, 2010; van Oers & Muller, 2010). Therefore, individual variation, whether as a product of phenotypic and/or genotypic constraints, could also have important implications on population dynamics.

1.5. The importance of quantifying CIDs in natural populations in the field

The majority of the research on CIDs in behaviour has been carried out in laboratory-based environments (e.g. Mather & Anderson, 1993; Bell & Sih, 2007; Dingemanse et al., 2007; Cote et al., 2010). Despite the importance of laboratory based research in developing our understanding and insight into how to test for CIDs in behaviour, there is evidence that caution should be extended to these results (Crabbe et al., 1999; Miller et al., 2005), and there is conflicting evidence as to whether or not these findings can be extrapolated to natural populations (Wilson et al., 1993; Wilson & Godin, 2009; Herborn et al., 2010). For example, Wilson et al. (1993) found that the shyness-boldness behavioural axis in pumpkinseed sunfish was stable between individuals when the fish were in their natural environment. However, after they were transferred to the laboratory CIDs in behaviour were seen to ‘disappear’ after a period of social and ecological isolation. Furthermore, others have cautioned that any link between CIDs in behaviour in the wild and captivity could be species specific (Minderman et al.,

2009; Minderman et al., 2010; Herborn et al., 2010). Therefore, in order to ascertain the ecological and evolutionary relevance of CIDs in behaviour, it is important that we attempt to quantify them in the natural environment (Bell, 2005; Dingemanse & Réale, 2005; Twiss & Franklin, 2010; Briffa & Greenaway, 2011).

Despite the need to address whether or not CIDs in behaviour exist in wild populations, there are concerns over the feasibility of carrying out behavioural tests on individuals in an exclusively field environment. The primary concern is that it is not possible to control environmental variables; therefore, different individuals may experience different environmental conditions and the same individuals may experience different environmental conditions across repeated measures. Consequently, individuals may show different responses to a behavioural test as a result of the specific micro-environmental conditions they experienced prior to and/or during the behavioural tests. However, this problem has also been shown to occur under laboratory conditions (Benus & Rondigs, 1996; Crabbe et al., 1999; Miller et al., 2005), which to a large extent has been overlooked. Despite these concerns over the influence of environmental conditions on behaviour, there have been a growing number of studies carrying out behavioural experiments solely in the field (e.g. Coleman & Wilson, 1998; Réale et al., 2000; Réale & Festa-Bianchet, 2003; Brown et al., 2005; Martin & Réale, 2008a, b; Minderman et al., 2009; Minderman et al., 2010; Briffa & Greenway, 2011; Twiss et al., 2011a).

A common approach to in-field behavioural tests is to manipulate behaviour either using a novel stimulus (i.e. the exploration-avoidance behavioural axis; e.g. Martin & Réale, 2008b; Twiss et al., 2011a) or non-novel stimulus (i.e. the shyness-boldness behavioural axis; e.g. Coleman & Wilson, 1998; Briffa & Greenway, 2011). However, where wild studies involve the manipulation of behaviour, habituation and sensitisation to the behavioural tests needs to be considered (Martin & Réale, 2008b; Ellenberg et al., 2009). Furthermore, in the case of the novel stimulus the degree to which a manipulated behaviour is elicited may not be representative of the degree to which the same behaviour is elicited under ‘natural conditions’ (Twiss et al., 2011b). Therefore, it is important to consider whether or not a novel (and indeed, a non-novel) behavioural test is likely to result in an ecological and evolutionary meaningful conclusion.

Nevertheless, if behavioural tests do show that CIDs in behaviour do occur in natural populations then it is fundamentally important that the fitness consequences of these CIDs in behaviour are quantified. However, in order to obtain measures of fitness it is often necessary to disturb and/or capture individuals, which can also result in habituation and sensitisation (Réale et al., 2000; Réale & Festa-Bianchet, 2003; Martin & Réale, 2008b; Ellenberg et al., 2009). Consequently, the trade-off between acquiring detailed measures of an individual's fitness (or fitness proxies) whilst minimising the impact on the individual's natural behaviour can be difficult to balance. However, for some studies where detailed and accurate information is required (e.g. age and relatedness of individuals), there are arguably no alternatives to disturbing and/or handling individuals.

Given the importance of understanding how an individual's phenotype and genotype affects their fitness, there are no studies (that Ross Culloch (RMC) is aware of) that have attempted to use a strictly 'hands-off' observational approach to ascertain whether or not CIDs in behaviour exist in undisturbed wild populations. Furthermore, there are few studies that have attempted to balance these trade-offs by minimising disturbance and maximising data collection on individuals' 'natural' behaviour. For example, Twiss & Franklin (2010) collected behavioural observations on male grey seals (*Halichoerus grypus*) on a breeding colony over two consecutive breeding seasons. Using these observational data, they showed that CIDs in the 'alert' behaviour occurred across the two breeding seasons. These individuals were handled twice (once during the early stages of their tenure on the colony and once during the later stages) and the resulting data were used to show that consistency in behaviour was not related to various fitness proxies. With this exception no other studies (that RMC is aware of) have attempted to address whether or not CIDs in behaviour occur in wild populations by using behavioural data gathered from individuals that were not subject to behavioural tests. From a pragmatic research perspective, this approach makes biological sense. Specifically, it seems appropriate to first identify whether or not CIDs in natural behaviour do occur, and then use intrinsic (e.g. body mass, body size) and extrinsic (e.g. social and environmental) covariates to attempt to 'explain

away' these consistencies as products of either individuals' state or the micro-environmental stimuli that individuals' experience.

1.6. Aims

Using observational studies, this thesis aims to address whether or not CIDs in behaviour exist in a natural population of wild animals. To-date, very few studies have attempted to quantify CIDs in behaviour using only an observational approach (Twiss & Franklin, 2010). Therefore, this work aims to strengthen the evidence for CIDs in natural populations (Twiss & Franklin, 2010) and therefore provide further evidence for CIDs in behaviour that have recently been observed with the more commonly used laboratory-based approaches (Mather & Anderson, 1993; Bell & Sih, 2007; Dingemanse et al., 2007) and in-field behavioural experiments (Coleman & Wilson, 1998; Briffa & Greenway, 2011; Twiss et al., 2011a).

To address whether or not CIDs in behaviour do occur in a natural population of wild animals, observational data were collected on postpartum female grey seals during three consecutive breeding seasons. This study system was chosen because female grey seals are individually identifiable (from natural markings; Redman, 2002), individuals typically return to the breeding colony within a few days of the previous years' pupping date (Pomeroy et al., 1999) and they typically return close to their previous years' pupping site (Pomeroy et al., 1994, Pomeroy et al., 2000a, Pomeroy et al., 2005). Females give birth to one pup (meaning there is no sibling conflict or partitioning of resources) and will spend on average 18 days nursing their pup (Pomeroy et al., 1994), during which time they will not return to the sea to feed (Pomeroy et al., 1999). On approximately day 16 of lactation the female will enter oestrus (Pomeroy et al., 1999; Twiss et al., 2006), at which point she will mate with one or more males before returning to the sea (Twiss et al., 2006). Therefore, as it is possible to gather detailed behavioural observations on the same individual within a breeding season and potentially over subsequent breeding seasons this is an ideal study system for investigating the presence of CIDs in the behaviour of a natural population of wild animals.

The present study will use scan samples gathered at 5 minute intervals (Chapter 2, Section 2.5.4) to quantify repeatability in behaviour. No previous study (as far as RMC is aware of) has looked for evidence of CIDs in behaviour at such a fine temporal scale. Using modern statistical techniques, an approach for analysing such data shall be presented. Ultimately, this general approach can be applied to similar observational studies, and it could also be applied to other temporally fine-scale datasets examining a broad range of behavioural traits, such as movement patterns, habitat use and site fidelity (e.g. Deutsch et al., 2003; Hoffman et al., 2006; Wolf & Trillmich, 2007), social interactions (e.g. Sousa-Lima et al., 2002; Antunes et al., 2011; Trimble & Charrier, 2011) and diet and foraging specialisations (e.g. Cherel et al., 2007; Foote et al., 2009; Newsome et al., 2009). Therefore, the analytical approach presented in this thesis should be of interest to a broad range of behavioural and evolutionary ecologists looking to quantify repeatability in a broad range of behavioural traits.

Finally, observational data were also gathered on postpartum female grey seals that are part of an on-going long-term reproductive study, which is carried out on a different geographic region of the same breeding colony. Using this independent dataset the influence of individual variation in behaviour on commonly used short-term proxies of fitness shall also be addressed. This is of particular interest to researchers in this field of behavioural and evolutionary ecology, as more and more empirical studies have shown that there are fitness consequences associated with individual variation in behaviour. Specifically, certain behavioural types (e.g. individuals that are consistently less aggressive) have been shown to fare better under particular environmental conditions (Ellenburg et al., 2009; see also Section 1.5).

Ecological data is typically subject to measurement error and process noise (Bolker, 2008). The first of these is the variability (or noise) that occurs when measurements are taken. This error makes it hard to estimate parameters and to make inference about ecological systems. Consequently, this can lead to large confidence intervals and low statistical power. The second of these is made up by demographic and environmental stochasticity and is a real part of the ecological system (Bolker, 2008). Furthermore, given the nature of ecological data, they often

violate one or more of the underlying assumptions of commonly applied statistical approaches (Zuur et al., 2009a). Typical issues include zero-inflation, autocorrelation (lack of independence), collinearity of covariates and pseudoreplication. Ignoring these issues can lead to severe problems with inference (e.g., increasing type I or type II errors, which can potentially result in the wrong ecological conclusion). Despite these issues being well documented, many studies still fail to address them (Bolker et al., 2009; Zuur et al., 2009a; Zuur et al., 2009b). Consequently, in order to assess whether or not these aforementioned statistical issues pertain to the datasets used in this thesis, a thorough exploratory analysis was undertaken (Chapter 3), prior to carrying out the desired analyses.

The exploratory analysis showed that for some of the behaviours of interest the data violated some of the assumptions of these commonly adopted statistical approaches. Consequently, in order to apply these statistical approaches to these datasets and still have confidence in our biological conclusions, it was necessary to implement a robust three-step analytical approach, where each step supported the findings of the subsequent step(s). The three steps are as follows:

1) Using the intraclass correlation coefficient (ICC) to identify whether or not CIDs in behaviour occur, irrespective of the influence of social and/or environmental factors. Specifically, this analysis uses the proportion of time spent in behaviour *x* (e.g. aggression) and tests for correlations across breeding seasons. Therefore, this step uses data collected on an inter-annual temporal scale (Chapter 4).

2) Using generalised linear models (GLMs) the individuals' unique identification code (individuals' ID) shall be included in the model as a fixed-effect, along with other covariates that are thought to (or are known to) influence behaviour on grey seal breeding colonies. This step of the analyses aims to identify which covariate(s) (including individuals' identity) best explain the variance in behaviour within a breeding season by using the temporally fine-scale datasets (Chapter 5). If individual's ID is retained in the model, then this indicates that there is considerable between-individual (and therefore limited within-individual) variation in behaviour within a breeding season, which is a pattern indicative of repeatability (Lessells & Boag, 1987; Bell et al., 2009).

3) Next, using generalised linear mixed models (GLMMs), the individuals' ID is included as random-effect whilst the other covariates (that were included in step 2 of the analyses) are again included as fixed-effects. By using this approach, inference can be made on the extent to which the variation in behaviour *x* not explained by the fixed-effects is attributed to differences between individuals within the population (Pinheiro & Bates, 2000). In other words, an estimate that represents the proportion of variation for each individual, which is independent of the fixed-effects, can be extracted from the GLMMs. Using the ICC (employed in step 1), the repeatability of these estimates for individuals re-sighted across breeding seasons can be quantified (Chapter 6). Therefore, using the combination of the GLMMs and the ICC it is possible to incorporate the influence of social and environmental factors whilst quantifying whether or not CIDs in behaviour do occur. However, for some of the behaviours of interest, the data violated certain assumptions pertaining to the GLMMs. Consequently, the results from the previous two steps of the analyses are used to support the results obtained from step 3, and thus provide confidence in using GLMMs for identifying CIDs in behaviour (despite these datasets not satisfying all of the caveats and limitations).

Subsequently, to assess how robust this approach is to variation in data collection protocols, the three-step analytical approach shall be applied to the independent reproductive study mentioned above. In this study, behavioural observations were intermittent throughout the breeding season and there were comparably fewer social and environmental data available for these known individuals. Nevertheless, it was expected that similar behavioural patterns would occur within different regions of the same breeding colony, despite variation in the data collection procedures between the two studies (Chapter 7).

Finally, to assess whether there are fitness consequences to CIDs in behaviour, the influence of the robustly repeatable behaviours (as identified in Chapters 6 and 7) on commonly used short-term proxies for fitness shall be addressed (Chapter 8). Once again, these analyses shall be carried out on the independent reproductive study, where additional reproductive covariates (e.g. pups daily growth rate, mother-pup mass transfer efficiency, maternal postpartum mass, mothers daily mass loss) are available.

Chapter Two:
General methodology

2.1 Introduction

This chapter provides an introduction to grey seal breeding ecology and the North Rona (U.K.) breeding colony where the data presented in this thesis were collected. Since many of the methods are relevant to several chapters they will be presented here to prevent repetition throughout the thesis. More specifically, this chapter will describe and define the behavioural categories used during behavioural observations and it will give the rationale for the approaches used in data collection and data mining. Methods that are specific to particular chapters are not presented here.

Throughout this thesis boxplots show the lower quartile, the median, the upper quartile and the whiskers, which extend to the most extreme data point that is no more than 1.5 times the inter-quartile range from the box. Where null hypothesis significance testing (NHST) is used, $p \leq 0.05$ is considered significant. Figures and tables that have a prefix of 'A' can be found in the appendix of the relevant chapter. All statistical analyses were carried out in R (R Development Core Team, 2011).

2.2. The grey seal (*Halichoerus grypus*)

Grey seals occur along the temperate and sub-arctic waters of the eastern and western Atlantic coasts and in the Baltic Sea. Although there are many similarities across geographical regions, the subsequent account of the grey seal breeding season focuses on research carried out in the U.K. For specific information on Canadian colonies see Boness & James (1979) and for Baltic colonies see Jussi et al. (2008).

2.2.1. U.K. grey seal breeding ecology

In the U.K., grey seal breeding colonies are typically formed on remote uninhabited beaches or islands. The dates of the breeding season do vary depending on geographic location, but within a particular colony it is consistent. The breeding season in the U.K. extends from the beginning of September to early January, with individual colonies forming for approximately 8 to 10 weeks (Coulson & Hickling, 1964; Anderson et al., 1975). The dates for specific colonies generally follow a clockwise pattern, with the colonies in the south-west (such as those in Cornwall, south Wales and Ireland) breeding earliest, moving round the coast to colonies in the north-east of England (such as those on the Farne Islands and Donna Nook), which breed later.

Whilst on the breeding colony, access to water is important to females for thermoregulation purposes and may also be important for maintaining a positive water balance (Twiss et al., 2000; Redman et al., 2001; Twiss et al., 2001; Twiss et al., 2002). Consequently, females tend to colonise areas around pools of water or remain close to the shore (Boyd et al., 1962; Anderson et al., 1975; Pomeroy et al., 1994; Twiss et al., 2000). Individual females typically return to the breeding colony within a few days of the previous years' pupping date (Pomeroy et al., 1999) and give birth to one pup. During her time on the breeding colony the mother will generally stay in close proximity to her pup, either on land or close to the shore, depending on the topography (Harwood, 1976; Twiss et al., 2000). Once females have given birth they become aggressive towards one another (Bonner, 1981). Consequently, mothers tend to maintain a minimum distance of 2.5 m from their nearest female neighbour (Boness et al., 1982; Caudron, 1998; Twiss et al., 2000). Therefore, overcrowding which can make individual identification (Section 2.5.1) and behavioural observations difficult is not often a problem on grey seal breeding colonies. A female will spend on average 18 days nursing her pup (Pomeroy et al., 1994) and on approximately day 16 of lactation she will enter oestrus (Pomeroy et al., 1999; Twiss et al., 2006), at which point she will mate with one or more males before returning to the sea (Twiss, 1991; Twiss et al., 2006).

During this time on the breeding colony, females do not return to the sea to feed; instead they use energy reserves stored primarily in the form of a thick layer of blubber. This blubber layer is also used to provision the pup via milk that is very rich in fat, ranging from approximately 30% to 60% lipid content depending on the individual and the age of the pup (Pomeroy et al., 1996; Debier et al., 2003). Once pups are weaned they often move towards the outskirts of the colony to areas that remain uncolonised by adults (Twiss et al., 2001) and they stay on the colony for several weeks until their blubber reserves are considerably depleted, before they enter the sea (Bennett et al., 2007).

2.2.2. Site fidelity and local associations

Females have been shown to use the same breeding colony for up to 25 years (Pomeroy et al., 1999) and depending on the colony and the study, individuals have been shown to return within a median distance of 55 m, 39 m and 25 m of the previous years' pupping site (Pomeroy et al., 1994, Pomeroy et al., 2000a, Pomeroy et al., 2005). Furthermore, mothers tend to remain close to their pupping site throughout lactation and they rarely move further than 10 m from their pup (Redman et al., 2001; Redman, 2002). Despite this high degree of site fidelity and the limited variability in an individual's parturition date (Pomeroy et al., 1999) there is no evidence for genetic differentiation between the major breeding aggregations in different regions of the North Rona colony (Poland et al., 2008). However, the same study found that the relatedness of mothers within regions was significantly higher than the relatedness of mothers between regions, which suggests that females tend to be site faithful to the region of the colony where their natal site can be found. Nevertheless, the study found limited evidence of fine-scale kin clustering (at a 10 m x 10 m spatial resolution), and there was no significant kin clustering detected in the area encompassing the sub-section of the colony in which the data were collected for the current study (Poland et al., 2008; Section 2.3.2). Furthermore, within this region of the colony, neighbouring mothers that were likely to socially interact (given that they were on the colony at the same time and were in the same location) were no more related to one another than random (Poland et al., 2008). Therefore, it is unlikely that the social interactions of mothers on North Rona are influenced by kin selection; however, there is evidence

of non-kin based associations occurring within some areas on North Rona (Pomeroy et al., 2005).

Pomeroy et al. (2005) modelled the likelihood of female association in two years as a result of site fidelity, variation in parturition date and pupping site quality. They found that the number of mothers that pupped more than the median distance (> 40 m) from the previous year's pupping sites showed inter-annual associations that were considerably greater than the model predicted. Therefore, specific females were forming active associations and were 'choosing' to be near one another in successive years.

2.2.3. The breeding ecology of male grey seals

Grey seals generally have a polgynous mating system (Anderson & Fedak, 1985; Twiss, 1991; Twiss et al., 1998), where an individual male's mating success is directly related to the duration of his stay on the breeding colony (Anderson et al., 1975; Twiss et al., 1994). Breeding adult males show a greater degree of mobility over the colony than females, but their movements are confined to certain areas. The boundaries of these areas are not strictly fixed and males do not fully exclude other males, hence these are not territories in the formal sense (Twiss, 1991; Twiss et al., 1994). The individuals that occupy these areas are referred to as 'residents' (Twiss, 1991; Twiss et al., 1994). About one third of the adult male grey seals return to the breeding colony each year (Twiss, 1991) and although rare, individual resident males have been shown to use the same colony for up to 10 years (Twiss, 1991; Worthington-Wilmer et al., 1999). Males that do return have shown a high degree of site fidelity, with individuals returning within a median distance of 53 m to the centre of the area they occupied in the previous breeding season (Twiss et al., 1994).

2.3. The field site

The field site is located on the uninhabited island of North Rona (59° 06'N, 05° 50'W; Figure 2.1), which is approximately 75km NNW of Cape Wrath, Scotland. The island covers an area of approximately 1.2 km^2, rising to a height of

108 m above sea level. Although the island has remained uninhabited since 1885, farmers from Lewis have continued to graze sheep on the island. The grey seal breeding colony on North Rona was first noted in the literature by Harrison (1932) and Darling (1938) during the 1930s, but it is thought that the colony has been present since the 1840s. It was not until the late 1950s that the first research was carried out on the island's breeding population of grey seals (Boyd et al., 1962; Boyd & Laws, 1962).

The annual breeding season on North Rona stretches from late September to late November (Boyd & Laws, 1962). The peak in the number of pups occurs between the 8th-10th of October (Hewer, 1959; Hiby et al., 1996; Twiss et al., 2000), with 96% of pups born between 19th September and 29th October (Harwood et al., 1991). Pup production has gradually declined over the last decade, with an estimated 1,105 pups born in 2000 and 629 born in 2010 (Sea Mammal Research Unit (SMRU), unpublished data; see also Lonergan et al., 2011). The majority of the breeding seals are located on the Fianuis peninsula where about 95% of the colony's pups are born (Boyd & Laws, 1962). Previous studies have typically divided Fianuis into four areas, the Study Area (SA), Fianuis South (FS), Fianuis Central (FC) and Fianuis North (FN) (e.g. Pomeroy et al., 1994; Twiss et al., 1994; Redman, 2002; Poland et al., 2008; Figure 2.2). This division is based on topographical features and discontinuities in the general distribution of seals. Previous studies carried out research over the majority of the island (e.g. Boyd & Campbell, 1971), but almost all of the more recent research has focused on the SA.

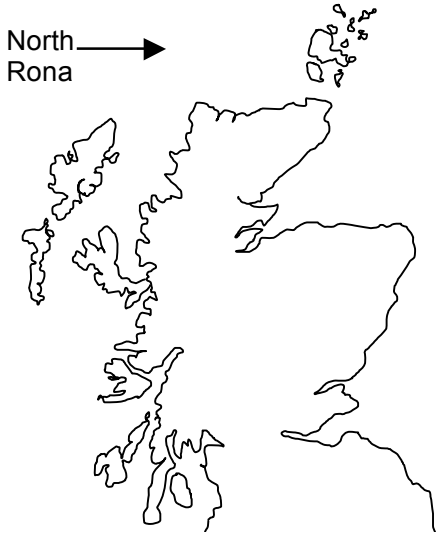


Figure 2.1: Location of North Rona in relation to the Scottish coast. Adapted from Redman (2002)

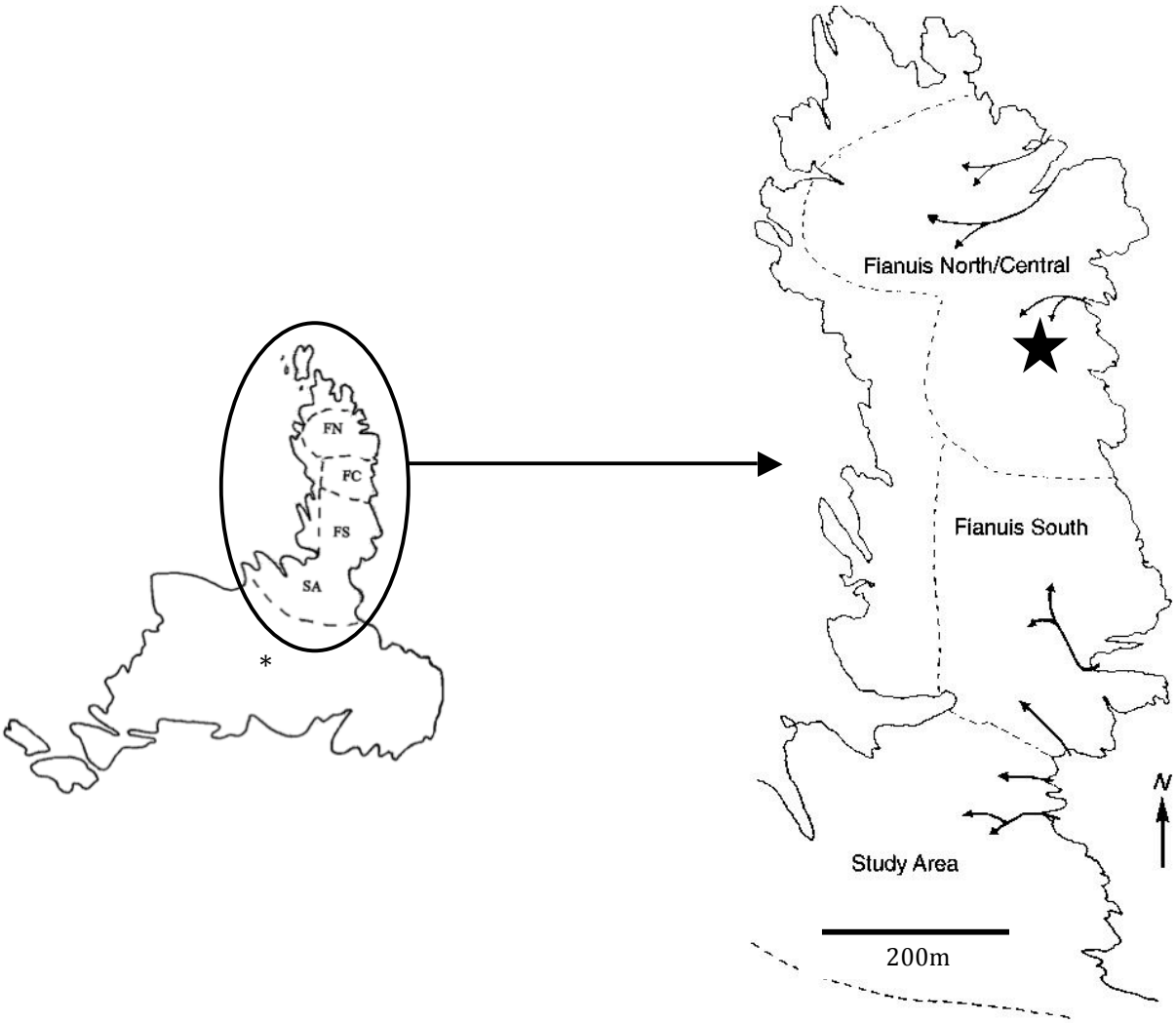


Figure 2.2: Map of North Rona showing the location of the Fianuis peninsula; * indicates the location of the hut where the field team stayed and where the equipment was stowed at the beginning and the end of the breeding season. Access points via gullies are on the east side and are marked by arrows. The study area (SA) is situated at the southern end of the peninsula. FN = Fianuis North, FC = Fianuis Central, FS = Fianuis South;★ indicates the location of the North Study Area (NSA; Section 2.3.2). Adapted from Redman (2002).

2.3.1. Research on North Rona

The long-term study of grey seals on North Rona has produced a wealth of information on grey seal breeding ecology (e.g. Boyd et al., 1962; Boyd & Campbell, 1971). More recently, research on North Rona has answered important questions on: individual variation in reproductive success (Twiss et al., 1998; Pomeroy et al., 1999); relatedness and paternity (Pomeroy et al., 2000b; Twiss et al., 2006; Poland et al., 2008), sociality (Pomeroy et al., 2005; Ruddell et al., 2007), sexual selection (Twiss et al., 2007), pup mortality (Twiss et al., 2003), recruitment rates (Pomeroy et al., 2010), colonisation patterns (Twiss et al., 2000; Twiss et al., 2001) and site fidelity (Pomeroy et al., 1994; Twiss et al., 1994; Pomeroy et al., 2000a, b; Pomeroy et al., 2005). In order to address some of the questions posed in these studies and the questions surrounding ongoing research, it has been necessary to handle the seals in order to obtain various samples (e.g. the weight of the mother and pup for energetic studies and tissue samples for molecular analyses). The handling and sampling procedures are well established and are detailed in Twiss (1991), Pomeroy et al. (1999) and Langton et al. (2011).

2.3.2. The study site

To observe the seals in as natural an environment as possible the study site had to be out-with the areas where seals were handled. In addition, to obtain an adequate sample size of individuals the study site also had to have a high density of females. Consequently, based on these prerequisites, the study site was located in the north section of the Fianuis peninsula, and will subsequently be referred to as the North Study Area (NSA). The NSA covered an area of approximately 0.06 km^2 (Figure 2.3). A hide was erected facing North-East overlooking the largest pool within the NSA. Data were collected in 2007, 2008 and 2009 (Section 2.4). The hide was erected in the same location in all three years. In 2008 the hide was demolished in storm force winds on 25th October. The remains of the hide were salvaged for repair or for scrap. For the remainder of the 2008 field season behavioural observations were carried out from a tent, which was in a different location (because the lower vantage point of the tent meant that the location of the hide was not suitable, Figure 2.3).

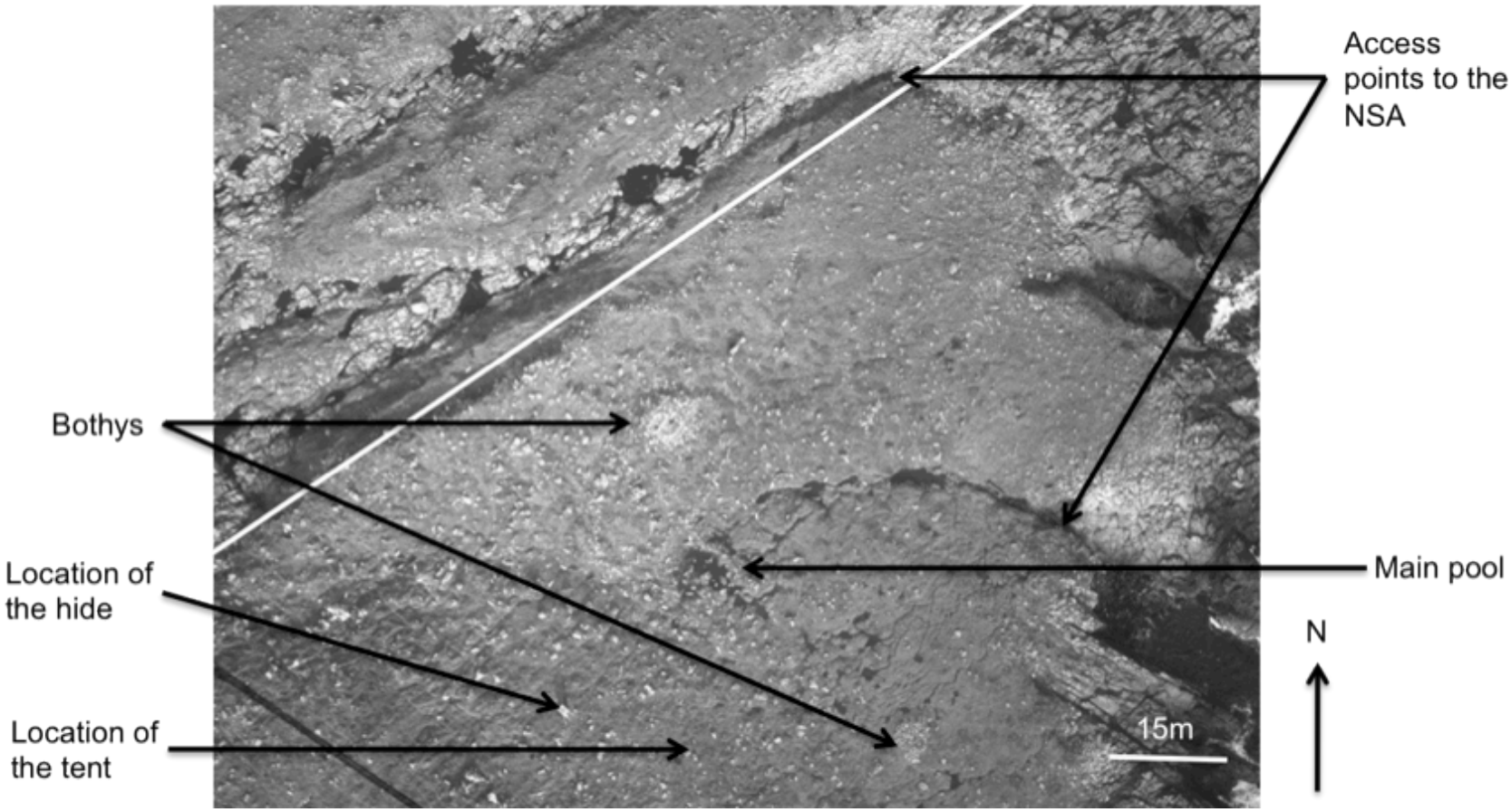


Figure 2.3: A print of a digitised aerial photograph of the North Study Area (NSA). The location of the hide (for all three field seasons) and the location of the tent that was used for the latter part of the 2008 field season are shown. Landmarks noted in the text are also shown. The area to the north west of the white line was out-with the field of view from the hide (image courtesy of Callan Duck, SMRU).

At a coarse scale, relative to a grey seal, the majority of the land in the NSA was flat. There were two steep-sided gullies lying to the North and East, both of which were used by the seals as access points to the colony. Within the boundary of the NSA there were two old bothys, both of which had the remains of a wall surrounding the ruins of the building. There were many other rocks and shallow gullies within the boundary of the NSA that were useful landmarks to assist in locating and mapping seals (Section 2.5.5). The key features listed above are all visible on a print of a digitised aerial photograph of the NSA (Figure 2.3) and the series of photographs (Figure 2.4), which illustrate the field-of-view from the hide. The majority of the NSA was covered in grass, but over the course of the breeding season the grass typically wore away through a combination of the movement of the seals and rainfall, which resulted in muddy and damp areas, particularly around pools.

The hide was deliberately situated very close to the study animals to allow for detailed observations of behaviours. During the peak of the breeding season females with pups were, on occasion, within one body length (approximately 2 m) of the hide. In order to minimise the disturbance to the seals the approach to the hide was always made quickly and quietly, taking wind direction in to account. Once in the hide preparation for data collection took on average 10 min. This was considered to be a suitable length of time to allow any individual that may have been disturbed by the approach to return to their previous state. From qualitative observations mothers that were disturbed on approach typically carried out head-up ‘Alert’ behaviours in the direction of approach. In these instances the females typically returned to their previous state within a minute or two. Additional caution on approach was required if a male or a pregnant female was within approximately 10 m of the hide, as these individuals often reacted by moving quickly in the opposite direction of approach, which could cause considerable disturbance to the NSA. Under these circumstances the individuals’ position and behaviour were also taken into consideration when approaching the hide. If any individual did cause additional disturbance to the NSA then behavioural observations did not begin until the resultant disturbance was judged to have passed. This rarely took longer than 10 min.

Figure 2.4: Photographs of the NSA. Photographs **a)**, **b)** and **c)** are taken from left to right from inside the hide, respectively. Photograph **a)** shows the more northerly access point in the background and the northerly bothy and wall in the foreground; photograph **b)** shows the main pool; photograph **c)** shows the more southerly access point in the background. Photograph **d)** shows the hide in position and overlooking the NSA.

2.4. Fieldwork dates

The dates spanning the period of observations for the 2007, 2008 and 2009 field seasons are shown below, with the date of departure of the field team from North Rona in parentheses. All data were collected on British Summer Time (BST).

30th September 2007 – 1st November 2007 (4th November)
30th September 2008 – 31st October 2008 (3rd November)
30th September 2009 – 1st November 2009 (4th November)

There were three additional hides erected for use by other members of the field team, all of which overlooked the SA (Figure 2.2). The hide at the NSA was always first to be dismantled because of the distance to the storage point (approximately 0.8 km; Figure 2.2). In all three years, after dismantling the hide, presence/absence data were collected daily on known females that had not left the NSA before behavioural observations were completed for the season.

2.5. Data collection and analyses

The data used in this thesis were collected from the hide during daylight hours and were in four forms: 1) photographs for photo-identification, 2) behavioural observations using both scan sampling and focal sampling protocols (Altmann, 1974), 3) spatial data and 4) weather data. A field notebook was also used to record additional data *ad libitum*. Given the remote field site both the behavioural observations and the spatial data were recorded on paper and were entered into the relevant databases at the end of the field season. Only data from postpartum females are included in the analyses. If data were collected on known individuals before they gave birth it was omitted from all analyses.

2.5.1. Photo-identification

Photographs of individuals were taken using a digital SLR Canon EOS 30D with a Canon EF 100-400mm f4.5/5.6L USM image stabilised lens. Photographs

for photo-identification purposes were taken of every seal that entered the NSA, both left and right hand side photographs were taken if possible, and particular attention was paid to the flank, neck and head (Hiby & Lovell, 1990; Redman, 2002; Beaumont & Goold, 2007). The majority of females could be individually identified from their pelage markings, the males were more difficult to identify as their pelage was often relatively uniform and dark, and although it was not the primary focus of the study, keeping track of males was important for gathering data on male-female interactions between known individuals.

If behavioural data were collected on a female she was given a unique alphanumeric identification code. At the end of the 2007 breeding season a photo-identification catalogue of known females was created. Each entry contained the following information: the alphanumeric identification code from that breeding season, the date the female gave birth, the geographic location of where she gave birth (see Section 2.5.5), drawings of distinguishable features (if deemed necessary; Redman, 2002) and at least one photograph of both sides of the individual (if available). The catalogue was used in subsequent field seasons to identify returning individuals. At the end of each field season the catalogue was updated. An example of the photo-identification catalogue is shown in Figure 2.5. At the end of the study all individuals were given a final identification number; for recaptured individuals the final identification numbers started from 900 and for individuals that were seen in only one year they ranged from 1 to < 900.

From birth grey seal pups have a white fur coat that is typically kept until around the time of weaning, at which point the pup begins to moult and the juvenile pelage becomes visible. Therefore, for the majority of a mother's time on the colony her pup cannot be photo-identified because it does not have any distinctive pelage markings (Redman, 2002). Nevertheless, it is almost always possible to keep track of mother and pup pairs because the colony is not overcrowded and mothers tend to stay relatively close to their pup (Twiss et al., 2000; Redman et al., 2001; Redman, 2002).

Figure 2.5: Two examples of an entry in the photo-identification catalogue. Both females were seen in all three years, the unique identification code for each breeding season is shown on the top right hand side. Each entry has a table of basic information for each breeding season the individual was re-sighted. The best photographs for identification purposes are shown and a space for drawings and notes are also provided to assist with making positive identifications whilst in the field.

2.5.2. Activity budgets

Behavioural data were gathered on females, males and pups. If an individual was not in view during behavioural observations, then it was recorded as out-of-sight. The data collected on the males is not presented in this thesis, and will not be discussed further. Behavioural data recorded on the pups of known mothers were used in the analyses presented in subsequent chapters. Using scan and focal sampling protocols (Section 2.5.4) the activity budgets of female grey seals were calculated as the percentage of time spent in each of the behavioural categories whilst in sight. Therefore, the proportion of time spent out-of-sight was not included in the activity budget; however, it was taken in to consideration when investigating potential outliers (Chapter 3, Section 3.4.1).

2.5.3. The behavioural categories

There were a total of 21 behaviours that were recorded during observations of females. However, preliminary examination of the data found that some behaviours were recorded infrequently, resulting in small sample sizes for these particular behaviours. Consequently, the behavioural data were divided into nine distinct behavioural categories. The names, the definitions and the behaviours that form each of the nine behavioural categories are listed below. The code used to refer to the name of the behavioural category throughout the thesis is in parentheses.

Resting (R) – The female is in a non-active state lying with her head on the ground, her eyes may be open or closed.

Comfort Movement (CM) – The female makes adjustments to her position and/or shuffles her body on the spot, but remains in the same geographical location. The female may also scratch herself with her flippers.

Pup Check (PC) – The female gives a definite, distinct and directed look to her pup. The behaviour prior to this can range between subtly raising the head a short distance from the ground to the head being raised and the neck fully extended.

The former description is more likely to occur if mother and pup are in close proximity and appropriately orientated, whereas the latter is more likely to occur if the pair are not in close proximity.

Alert (A) – The female is aware, she may be looking all around her or in the direction of a perceived threat, typically the female will have her head up and her neck extended. This can appear similar to a 'Pup Check' with the important distinction that the female is not looking at or towards her pup.

Locomotion (L) – The female changes her geographic location. This behaviour may involve the use of the fore-flippers (for forward or backwards motion), 'barrel' rolling or shuffling (for sideward's motion; note the distinction between shuffling on the spot (see 'Comfort Movement'), and shuffling to change geographic location). This behavioural category excludes chasing behaviours (see 'Aggression').

Presenting & Nursing (MP) – The female lies on her flank exposing her nipples to the pup ('Presenting'), the mother is considered to be 'Nursing' when the pup makes oral contact with a nipple. These two behaviours were combined because it was not always easy to assess whether or not the pup was making oral contact with the nipple; this was especially true if the female had her back to the hide. This behavioural category represents time spent in behaviours that are associated with energy transfer to the pup.

Pup Interactions (PINT) – The female physically interacts with her pup, this includes (but is not limited to) nosing (touching the pup with her nose) and flippering (using her flipper to 'stroke' the pup). This excludes both presenting and nursing behaviours (see 'Presenting & Nursing'). This behavioural category represents time spent in behaviours that are associated with social interactions with the pup.

Aggression (AGG) – The female interacts aggressively, typically towards a conspecific, although aggressive behaviours were also recorded towards sheep and birds. This category includes but is not limited to; wailing (a vocal threat); aggressive flippering (the female vigorously 'waves' her flipper towards the

perceived threat, she may make contact); slapping (the female will lie on her side and continuously slap her flipper against her flank); open mouth threats (the female will open her mouth baring her teeth at the perceived threat); lunging (the female extends her neck, lunging towards the perceived threat, this typically follows an open mouth threat); biting (if the female makes contact she attempts to bite, this typically follows a lunge) and chasing (the female chases the perceived threat, this is the same as 'Locomotion' but with the clear intent on chasing a conspecific, or other perceived threat).

Sex (SEX) – A male mounts or attempts to mount the female. The male uses his jaws to grip the female by the neck and uses his fore-flippers to grip her body. Copulation attempts may be unsuccessful; this can occur if the female is unreceptive (typically resulting in aggressive behaviours on the females' part). A successful copulation occurs when intromission is clearly achieved and the copulation proceeded, uninterrupted, to completion (Twiss et al., 1998). Sexual behaviours typically occur at the end of lactation when a female's behaviour is likely to be motivationally different from maternal care prior to oestrus. Consequently, these behaviours were considered to indicate the point of transition between maternal care and the quick process of mating, weaning the pup and leaving the colony. Given that the focus of the present study was on maternal behaviour, the 'Sex' behavioural category was excluded from any additional analyses. However, in order to give a proportional representation of time spent in each behavioural category whilst on the breeding colony the 'Sex' behavioural category was included in the calculation of the activity budgets.

Previous studies investigating female grey seal behaviour have used similar behavioural categories. However, there are some variations within the literature, for example; Anderson & Harwood (1985) included the 'Alert' behaviour but did not mention the 'Pup Check' behaviour. It is therefore likely that they included 'Pup Check' within the 'Alert' behavioural category. Conversely, other studies have distinguished between the two behaviours (Kovacs, 1987; Haller et al., 1996; Caudron, 1998; Twiss et al., 2011). Anderson & Harwood (1985) also separated behaviours classified as 'Comfort Movement' in the present study in to two separate behavioural categories, 'Scratch' and 'Change Position'.

The decision to combine the 'Presenting' and 'Nursing' behaviours in the present study was necessary in order to prevent misclassification of the two behaviours. However, other researchers have defined 'Presenting' and 'Nursing' as separate behaviours (Kovacs, 1987; Haller et al., 1996). Kovacs (1987) stated that "time spent moving between nipples was included as part of the nursing sequence", which allows for a more straightforward classification of 'Nursing' if it is not clear whether the pup is making oral contact with the nipple or not. Haller et al. (1996) were quantifying energy investment on ice-breeding grey seals (Nova Scotia, Canada); therefore, differentiating between 'Presenting' and 'Nursing' behaviours was fundamentally important for this particular study. In order to obtain accurate data on whether individuals were 'Nursing' or not Haller et al. (1996) carried out simultaneous observations from 3 hides situated around their study site, which "provided virtually complete visual coverage of the surrounding ice". By doing this Haller et al. (1996) presumably minimised misclassification of the 'Presenting' and 'Nursing' behavioural categories in situations where mothers had their back to the hide, which was a regular occurrence in the present study.

Pup behaviour was grouped into 6 behavioural categories: 'Resting', 'Comfort Move', 'Alert', 'Locomotion', 'Mother Interactions' and 'Nipple Nosing & Suckling'. The first four are synonymous with the female behaviours, 'Mother interactions' are the same as 'Pup Interactions' with the obvious distinction that in this instance the behaviours were performed by the pup. The final behavioural category is the pups' equivalent to the 'Presenting & Nursing' behavioural category for the mother. The 'Nipple Nosing' behaviour occurs when the pup has its nose at the nipple and 'Suckling' occurs when there is clear oral contact with the nipple. The pup behavioural categories were summarised further, as inactive ('Resting'), active ('Comfort Movement', 'Alert', 'Locomotion') or interactive ('Mother Interactions' and 'Nipple Nosing & Suckling'). It is acknowledged that the interactive behaviours are confounding, for example, if the mother is 'Presenting & Nursing' then the pup must be 'Nipple Nosing & Suckling'. Therefore, the interactive behaviours will be dealt with appropriately, depending on the question(s) being posed. Henceforth the behavioural categories are not written within inverted commas and nor are they capitalised.

2.5.4. Behavioural observations

Behavioural observations were carried out from the hide from dawn to dusk on all days, with the exception of when other field studies required assistance from all members of the field team or during unsafe weather conditions (e.g. during extreme storm force winds). The principal method used for gathering behavioural data in all three years was instantaneous scan samples (Altmann, 1974). These were carried out at 5 min. intervals over 30 min. periods in 2007 and continuously in 2008 and 2009. Scan samples were always completed within a minute and every effort was made to keep the order in which individuals were scanned invariable so that the interval between subsequent scans was kept as consistent as possible. These data were gathered on all seals within the study area irrespective of their sex or age class. However, at the peak of the breeding season it was not always possible to scan every individual, therefore, priority was given to re-sighted mothers and their pups (i.e. females that had been recorded in previous breeding seasons) followed by unknown mother-pup pairs.

Previous studies investigating grey seal behaviour have used instantaneous scan sampling techniques with intervals ranging from 1 to 20 minutes (Harwood, 1976; Anderson & Harwood, 1985; Boness, 1984; Haller et al., 1996; Twiss 1991). However, with the exception of Twiss (1991), none of these studies addressed the minimum number of scan samples required in order to obtain an accurate representation of a grey seals' activity budget. Incidentally, within the field of behavioural ecology in general, very few studies consider the importance of addressing this issue (e.g. Engel, 1996; Wilson et al., 2008; Liu et al., 2010). When selecting the appropriate interval between sampling points it is inevitable that there will always be trade-offs involved (Altmann, 1974; Engel, 1996; Wilson et al., 2008). In the current study, shorter intervals were preferred in order to maximise the amount of data collected on individuals. This decision was based on Twiss's (1991) suggestion that a minimum of 180 scan samples were required to give an accurate representation of male grey seals' behaviour. Assuming that a similar number would be required for females, then approximately 3 complete days of continuous scan samples at a 5 min. interval would be required to obtain the minimum number of scan samples per individual. Therefore, in order to obtain

considerably more scan samples than the minimum, intervals longer than 5 min. would not be suitable since individual females' are only on the colony for a relatively short period of time (ca. 16 days, Pomeroy et al., 1999). Also, 5 min. intervals allowed adequate time between scans to gather additional data (such as spatial data (Section 2.5.5) and photographs for photo-identification (Section 2.5.1)). It is acknowledged that there are potential issues with shorter intervals resulting in temporal autocorrelation, which would result in a lack of independence between data points (Hurlbert, 1984; Zuur et al., 2009a, b). These issues are addressed and discussed in detail in Chapter 3, Section 3.12 as part of the exploratory analyses.

During the 2007 breeding season 30 min. continuous focal samples (Altmann, 1974) of known individuals were also collected in an effort to identify which of the two approaches (scan sampling or focal sampling) was best suited for collecting the behavioural data required to address the questions posed in this thesis. The focal samples were interspersed with the scan samples, with an average of five focal samples evenly dispersed throughout a day in order to control for any potential diurnal variation in behaviour.

Not all females within the NSA in 2007 were the subject of focal samples and those that were included were selected at random. The group of females that were used in focal samples never exceeded 10 individuals at any one time. To prevent observer bias (for example, the observer selecting females that were active rather than resting) the focal female was selected at random immediately prior to the focal sample. Once an individual was sampled it was excluded from the subsequent random selection process until all individuals within the group had been sampled. This was done to minimise variation in sample sizes between individuals. For the focal samples there were data collected on 26 individuals, with a median of 6 focal samples per individual (min. = 1; max. = 10), and for the scan samples there were data collected on 43 individuals with a median of seventy 30 min. periods of scan sampling per individual (min. = 1; max. = 125). Data were combined for all individuals to give a gross activity budget for each of the protocols. Using a paired t-test the two protocols showed a significant difference in the proportion of time spent in the comfort movement ($t = 3.913$, $df = 21$, $p =$

0.0008) and pup interactions (t =2.766, df = 21, p = 0.012) behavioural categories (Figure 2.6). In both cases the scan sampling protocol recorded a higher proportion of time spent in each of the behavioural categories. The other six behavioural categories were not significantly different (resting t = -1.821, df = 21, p = 0.083; pup check t = -0.822, df = 21, p = 0.42; alert t = 0.823, df = 21, p = 0.42; locomotion t = 1.962, df = 21, p = 0.063; presenting & nursing t = -0.381, df = 22, p = 0.707; aggression t = 1.484, df = 21, p = 0.153).

There are some outliers present in the scan sample data, in particular, the one individual that spent approximately 30% of their activity budget alert (Figure 2.6). If a minimum of 180 scan samples is applied here, the aforementioned outlier is dropped, but there is no change in the outcome in the pattern of the data or the significance of the t-tests, although the significance for the comfort movement and pup interactions behavioural categories do decrease considerably (t = 3.102, df = 18, p = 0.006; t = 2.252, df = 18, p = 0.037, respectively). It is not possible to apply such an *a priori* cut-off to the focal sample data as there are no previous studies addressing the required minimum time for observations in order to accurately represent a grey seals' activity budget. The results presented here suggest that for six of the eight behavioural categories the number of focal samples were adequate. For the comfort movement and for the pup interactions behavioural categories more focal samples may be required; however, these results may be a product of the sampling regime.

The behaviours comprising the pup interactions behavioural category may have been too infrequent to be recorded reliably by the number of focal samples carried out in the current study. The summary statistics of the focal sample data for the pup interactions behavioural category do appear to suggest that this was the case (min. = 0%, median = 0.18%, max. = 4.91%; Figure 2.6). However, when pup interactions did occur they were often in long bouts (Culloch, pers. obs.), which could explain why the scan sampling approach recorded a significantly higher proportion of time spent in this behavioural category. Given that the number of occurrences of pup interactions recorded during focal sampling was low, it is not possible to quantitatively test this supposition. However, further examination of the behavioural data for the female with the highest proportion of time spent

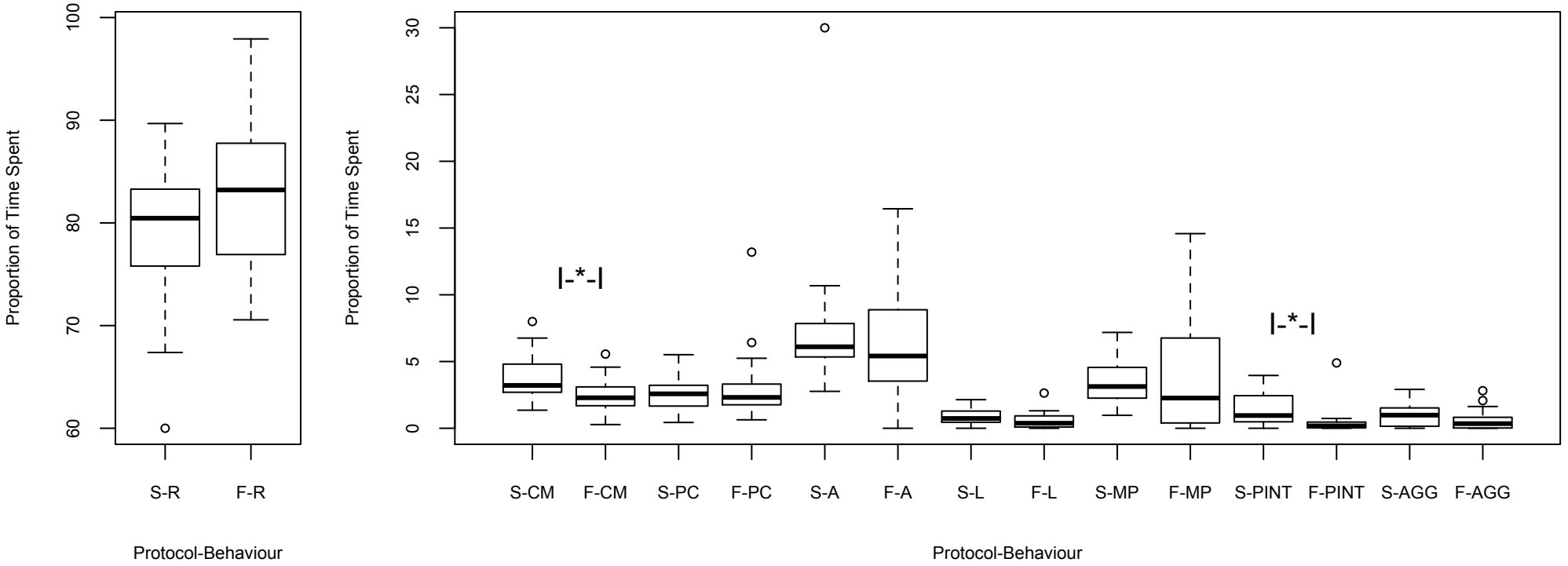


Figure 2.6: The behavioural data collected in 2007 showing the median proportion of time spent in each of the eight behavioural categories (R: resting; CM: comfort movement; PC: pup check; A: alert; L: locomotion; MP: presenting & nursing; PINT: pup interactions; AGG: aggression) using both the scan sampling (prefix 'S') and the focal sampling (prefix 'F') protocols. The results of the statistical analyses are shown in Section 2.5.4. Significant results are indicated by the **|-*-|** symbol.

interacting with her pup (4.91%) showed that she spent approximately 7 minutes during a (30 min.) focal sample, interacting with her pup. Of the 68 hours of focal sampling undertaken in 2007 this focal sample accounted for approximately 37% of the total occurrences of pup interactions recorded whilst using this sampling technique. Therefore, to reliably record pup interactions, it appears that a prolonged coverage (scan samples) rather than short bouts of detailed coverage (focal samples) is the more suitable sampling approach.

Behaviours comprising the comfort movement behavioural category occur relatively regularly and have bouts of variable durations. For example, some are typically short, such as scratching whilst others are typically longer, such as adjusting position. Although behaviours with shorter durations are more likely to be missed during scan sampling, the regularity of the behaviours coupled with those of longer duration may explain why the scan sampling approach recorded a significantly higher proportion of time spent in the comfort movement behavioural category. This supposition was tested using the focal sample data; however, contrary to the assumption, the majority of the occurrences of behaviours classified as a comfort movement were ≤ 5 seconds in duration (ca. 80%) with very few bouts lasting longer than 30 seconds (ca. < 1%). It is common for comfort movements to be interspersed with other behaviours over short durations (Culloch, pers. obs.), which may increase the probability of recording comfort movements during the 5 min. scan samples, despite their typically short duration. Although a more detailed analysis and comparison between the focal and the scan sampling data was not undertaken, it is expected that the results would have shown that the scan sampling protocol was over estimating the occurrence of comfort movement behaviours. It is also important to note that the findings presented here are taken from the gross data collected on a number of postpartum females. Therefore, if the two sampling techniques were compared at the individual level, they may not yield the same results.

It is likely that both sampling protocols will not be ideal for certain behaviours, and the comparison between the two techniques does suggest that this may be the case. Nevertheless, it was decided that focal sampling was not to be used in 2008 or 2009 and that a continuous scan sampling approach would be

better suited for this study. This was based on a number of reasons: important activity within the NSA was often missed; for example, the arrival of new individuals, aggressive interactions between individuals and individuals moving between locations. All of these scenarios typically resulted in the relocation of individuals, which can make keeping track of individuals problematic. The collection of additional data during focal sampling was not possible and this was especially awkward for: mapping seals at regular intervals, photo-identification of new arrivals, and positively identifying individuals already present within the NSA.

2.5.5. Spatial data collection and analyses

During the grey seal breeding season the SMRU carry out aerial surveys of all the established grey seal breeding colonies in Scotland for the purpose of estimating grey seal pup production (Hiby et al., 1988). Photographs are taken at approximately 366 m altitude on 5 x 4 inch format film using a Linhoff Aerotechnika camera with a 150 mm lens. Photographs are taken of the entire colony several times over the course of the breeding season. Courtesy of Callan Duck (SMRU), aerial photographs of the NSA were made available for all three breeding seasons. The photographs of the NSA were digitally scanned to a PC using an 'Epson Perfection V700 Photo' flatbed scanner at a resolution of 1200 dpi.

For all three years, prints of the same aerial photograph were used as a base-map of the NSA. During behavioural observations, the position, orientation and the identity of all the seals in the NSA were recorded on to a copy of the base-map. If the individual was not known, then the approximate age-sex group (adult male, adult female, juvenile, weaned pup, pup) was recorded on the map. In 2009, on the first map of the day the approximate age of all pups in the NSA was recorded (Figure 2.7; see Section 2.5.8 for details on how to age pups). Mapping of seals in the NSA was done approximately every hour in 2007 (due to the constraints of the sampling protocol), and done strictly at hourly intervals in 2008 and 2009.

After the field season each map was scanned (as detailed above) and the resulting digital images were rectified to real world distances in ArcInfo (ArcGIS

9.2 Environmental Systems Research Institute, Inc Redlands, CA). Geo-rectifying was done using Ground Control Points (GCPs) that were based on distances between landmarks identified both on the base-map and in the field. GCPs were located with reference to a 0,0 point (that was located close to the hide) using a Lecia Disto™ A3 laser distance finder (100 m range; accuracy +/- 1.5 mm). In the field, distances between landmarks throughout the entire area of the NSA were measured in metres. This was done at the beginning of the 2007 field season, before the NSA was colonised. After each map was rectified in ArcInfo the location of the seals were digitised into a new GIS point coverage using the rectified digital image of the map as a backdrop. The location of a seal was taken to be the location of the head (the tip of the arrow; Figure 2.7). A new coverage was created for every map. In ArcInfo every individual's location was assigned the following information: an identification code (if the individual was a female with a pup then the pup would have the same alphanumeric code as the mother but would be followed by '.1'; for example, 'A4' and 'A4.1'); the x and y coordinate for the location of the individual (calculated as metres from the 0,0 point); a 'type' code (this code gave information on whether the individual was known, their sex, their age-class, and in the case of females, their condition; for example known female with pup = 1; unknown female without pup = 4; female with dead pup = 6); the hour the map was taken; the day; the month; and the year. All of these data were required to efficiently mine and analyse the data in ArcInfo using custom written Arc marco language (aml) scripts.

Access to pools of water is important to females (Twiss et al., 2000; Redman et al., 2001; Twiss et al., 2001; Twiss et al., 2002; Section 2.2.1); therefore, all pools of water within the NSA were digitised for each breeding season. The pools were digitised as polygon coverages using the digital scans of the aerial photographs as a backdrop in ArcInfo. In 2007 and 2008 there were three aerial surveys carried out during the field season. In 2009, due to technical difficulties with the camera equipment there was only one successful aerial survey towards the end of the field season (Table 2.1). The seal coverages were assigned to pool coverages in 2007 and 2008 based on the mid-point interval between the dates of two consecutive aerial surveys. In 2009 the one pool coverage was used for the entire breeding season (Table 2.1). Given that rainfall

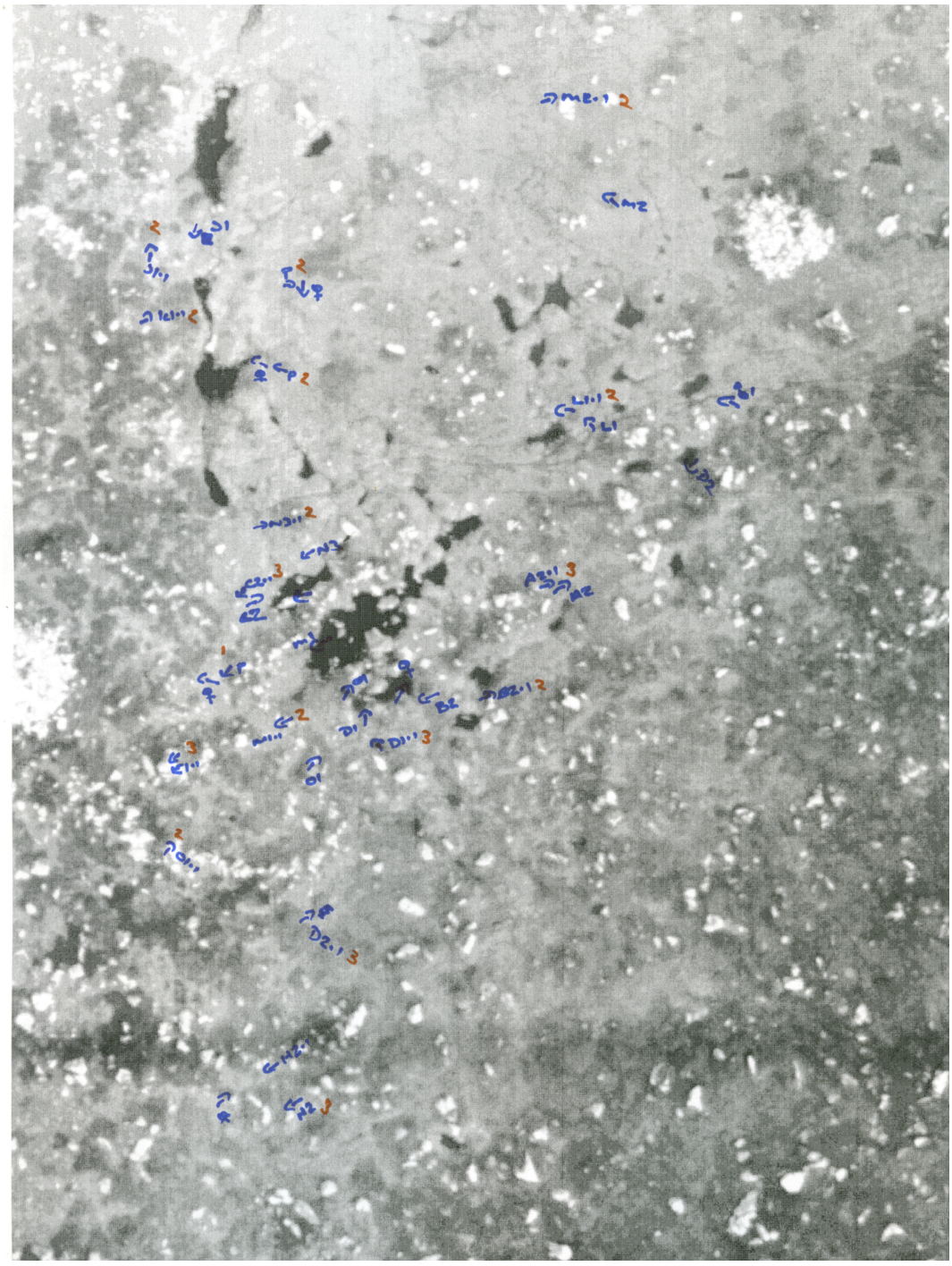


Figure 2.7: An example of the first map of the day from the 2009 field season with the pup stages are shown in orange next to the identification code (see Section 2.5.8 on how to age pups). The orientation of the seals was also collected (the arrow head indicates the direction the individual was facing). For the analyses presented in this thesis the location of the individual was defined as the head of the arrow and was digitised as a point. This map was taken on 19th October 2009 at 09:40.

is likely to be the most influential variable on the abundance, distribution and size of pools the rainfall data were also investigated as a potential basis for selecting which pool coverages were used with which seal coverages. For example, if heavy rain occurred after a dry spell just before an aerial photograph, the mid-point approach would over represent the availability of pools during the period prior to the aerial photograph. However, there was no such evidence that using the rainfall data over the mid-point approach would be preferential.

Table 2.1: The dates for the aerial surveys in 2007, 2008 and 2009 (YYYY/MM/DD). Pools in the NSA were digitised from all seven of the available aerial photographs. The start and end date (YYYY/MM/DD) of the seal coverages that were used in conjunction with each of the pool coverages are also shown.

Aerial Survey Date	Coverage Start Date	Coverage End Date
2007/10/04	2007/09/30	2007/10/09
2007/10/13	2007/10/10	2007/10/18
2007/10/25	2007/10/19	2007/11/01
2008/10/05	2008/09/30	2008/10/11
2008/10/17	2008/10/12	2008/10/23
2008/10/29	2008/10/24	2008/10/31
2009/10/24	2009/09/30	2009/11/01

On days with aerial surveys, photographs of the NSA and detailed field notes on the condition of the larger, more predominant pools were taken. These were consulted during the digitising of pools; however, it was still difficult to determine whether certain features were in fact pools or deep, shaded hollows. Therefore, any feature that was suspected to be a pool was digitised and was graded in ArcInfo from 1 to 5 based on the certainty of it being a pool (as judged by Ross Culloch). The grading was defined as follows: 5 = definitely a pool; 4 = highly likely to be a pool; 3 = most likely to be a pool; 2 = unlikely to be a pool; 1 = highly unlikely to be a pool. The polygon coverages, the aerial photographs and the photographs of the NSA were all used in the decision to omit pools with a grade lower than 3 from the subsequent analyses.

2.5.6. Data extracted from the GIS database

To select for a particular 'type' of individual (e.g., selecting only females) the numeric codes for those 'types' of individuals were used within the specific aml scripts. Mother and pup pairs were identified in the script by selecting the unique alphanumeric code for the mother and pup, then identifying the pup by the '.1' suffix. All data extracted from ArcInfo were output into text files. Specific commands used in ArcInfo that require additional explanation are described in the relevant sections below.

There were 6 variables extracted from the GIS database for each of the available maps, these were:

1) Distance between a mother and her pup (m).
2) Distance the mother was from the nearest pool (m).
3) Distance between a mother and her nearest female neighbour (m).
4) Density of females around a mother using a 10 m buffer zone. The size of the buffer zone was selected based on previous studies, which have shown that females rarely move more than 10 m from their pup (Redman et al., 2001).
5) A measure of home range usage. Kernel Density Estimation (KDE) was used to define an individual's home range using all of their mapped locations postpartum during the breeding season. Using the KDE, each point was assigned a value (ranging between 1 and 100, which represented the edge and the core of the estimated home range, respectively).
6) Inter-annual site fidelity was calculated using 4 metrics; distance between pupping sites between successive breeding seasons (m), distance between the centre of the core area of an individual's home range between successive breeding seasons (m), and the percentage of overlap between the 50% and 90% KDE isopleths (%) between successive breeding seasons. The site fidelity measures were calculated for consecutive years (2007 & 2008 and 2008 & 2009) and for non-consecutive years (2007 & 2009).

The first and second variables were selected because these are known to be important factors that influence a mothers' behaviour (Redman et al., 2001; Section 2.2.1). Consequently, females will regularly commute between pools of water and their pup (Twiss et al., 2000; Redman et al., 2001), especially if there are few pools (Redman et al., 2001). This movement between pool and pup is likely to influence an individual's home range usage, which is why variable 5 was extracted from the GIS database. Furthermore, movement on the colony will inevitably result in females interacting with neighbouring females. Therefore, the nearest neighbour and the density measures (variables 3 and 4) were also extracted. Finally, for re-sighted individuals, the site fidelity measures were extracted to assess whether the degree of site fidelity influences an individual's behaviour. For example, individuals that show a high degree of site fidelity may be more familiar with the terrain and/or neighbours, which could result in more time spent resting.

Point-to-point distance calculations were used to extract variables 1 and 3. For variable 2, the pools were converted from polygons to a matrix of high-density points set to 0.1 m real-world intervals that covered the entire area of the polygon. This was done because the point-to-line distance calculation did not differentiate between an individual that was near a pool or within a pool. Therefore, by calculating the point-to-point distance, if the distance was within the matrix threshold (≤ 0.05 m) then the individual was considered to be within a pool and the distance value was converted to 0. In order to calculate the density measures for variable 4 the individual was selected and a buffer zone of 10 m was created around the target female, and the number of females within this area was calculated (excluding the target female). All females were included in the density analysis, irrespective of whether they were pregnant, had a pup, or their pup was dead.

There is considerable debate over the best method for estimating home range (e.g. Seaman & Powell, 1996; Getz & Wilmers, 2004; Hemson et al., 2005; Börger et al., 2006; Horne & Garton, 2006; Fieberg, 2007; Getz et al., 2007; Lichti & Swihart, 2011). The minimum convex polygon (MCP) approach geometrically bounds the area containing all locations of an individual, which means that MCPs

are primarily defined by the longest distance movements (White & Garrott, 1990). This approach is often considered to be outdated, with the kernel density estimate (KDE) (Worton, 1989) and the local convex hull (LCH) (Getz & Wilmers, 2004) methods representing a substantial improvement over MCPs (Lichti & Swihart, 2011). Both KDE and LCH give a representation of relative spatial differences in the intensity of home range usage. However, both empirical and theoretical studies have produced conflicting results with respects to which of these two estimators performs best (Getz & Wilmers, 2004; Getz et al., 2007; Lichti & Swihart, 2011). Given the current debate over whether KDE or LCH is the better approach for estimating home range, it was decided to use KDE because, at present, it is the most commonly applied method for this purpose.

The KDE estimates the probability of an individual using an area as defined by a series of density isopleths. In the present study these isopleths were calculated at 5%, 10%, 50%, 90% and 95%, with the 95% isopleth representing an individual's core area. Consequently, each data point from all of the maps for an individual within a breeding season had a home range value ranging between 100 (the core area of their estimated home range) and 1 (the area of least usage within their estimated home range). The KDEs were extracted using the 'pointdensity' command available in the GRID package of ArcInfo. GRID is a raster-based module of ArcInfo, where a raster (which is also referred to as a grid) is defined as a matrix of cells organised into rows and columns, with each cell representing a value. Each point was counted once using the kernel function, which fits a smoothly tapered surface to each point. The shape of the area around each cell (also referred to as the neighbourhood) is always circular when using a KDE. The density is calculated using the number of points that fall within the neighbourhood of each output raster cell, divided by the area of the neighbourhood. This gives a smoother output grid, while maintaining the same general values for density (Silverman, 1986). Determining the radius of the output raster cell is an important and difficult issue when implementing a KDE (Silverman, 1986; Fieberg, 2007). A narrow radius allows nearby observations to have greatest influence on the density estimate, but if the radius is too narrow then spurious fine structure becomes visible. Conversely, a wide radius gives distant observations more influence, but if the radius is too wide then the bimodal nature of the distribution is

obscured (Seaman & Powell, 1996). The default option in ArcInfo allows all cells in the output grid to have at least one point within the radius. This option was not used because potential outliers would have had a considerable effect on the radius size. Consequently, the radius was set to 10 m, which was selected based on the same reasoning for the buffer zone size for the density data (see above, Redman, 2001).

For the site fidelity measures, the pupping site was defined as the X and Y coordinates of the female on the first map on the day that her pup was first seen. If the birth of the pup occurred during the day then the location of the mother was taken from the subsequent map. The centre of the core area of a female's home range was calculated as the X and Y coordinates of the location that was closest to the home range value of 100, and therefore closest to the centre of the core area. The site fidelity measures for these two variables were calculated as point-to-point distances (m). The overlap (m^2) of the 50% and 90% KDE between breeding seasons was calculated using the intersect command available in GRID. The percentage of overlap between the KDEs for the two breeding seasons was calculated by summing the total area (m^2) of the KDE isopleths for both years, calculating the area overlap, dividing the overlap by the total area and multiplying by 100.

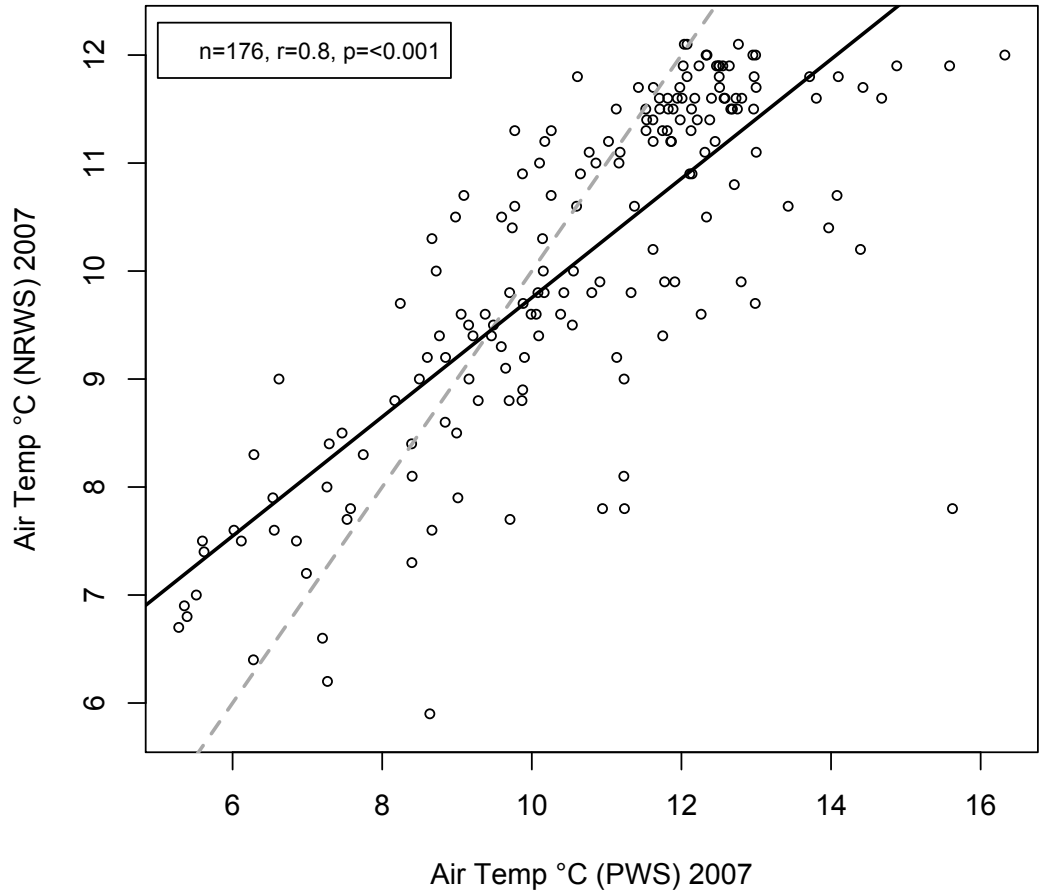
2.5.7. Weather variables

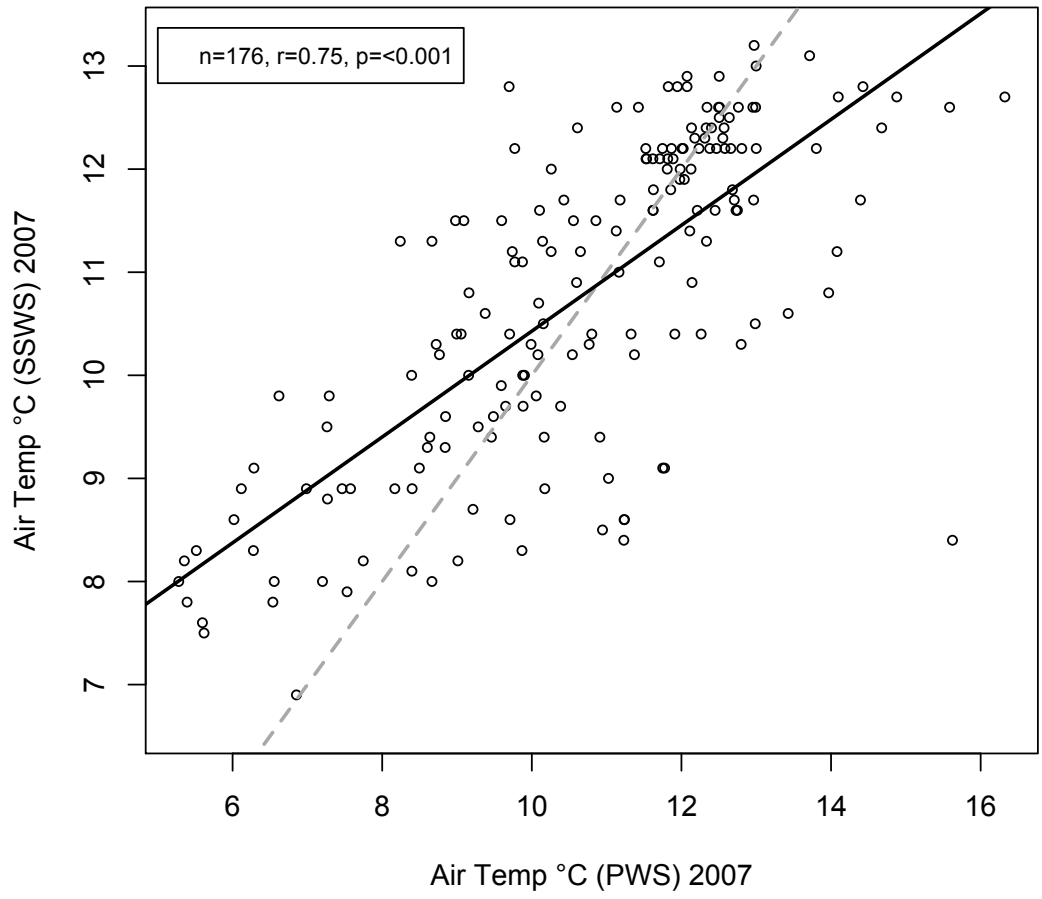
The weather parameters used in this study were air temperature (^oC) and rainfall (mm). The reasons for selecting these parameters relate to the importance of thermoregulation requirements to grey seals and the importance of the availability of water (Twiss et al., 2000; Redman et al., 2001; Twiss et al., 2001; Twiss et al., 2002). Although wind speed could potentially play a role in thermoregulation, the uneven terrain coupled with the seals being so close to the ground makes it difficult to accurately assess wind at a spatial resolution relevant to the seals. Therefore, to minimise the inclusion of variables that would give minimal additional understanding to the results presented in subsequent chapters wind speed is not considered further.

The weather data were collected using a DataHog2 (Skye Instruments Limited) in 2007, and a Nexus Professional Weather Station 35.1075 (TFA) in 2008 and 2009 (from here on collectively named as 'personal weather stations'). Each year weather data were collected at the finest temporal scales provided by the respective instruments, which were at 10 min. intervals in 2007 and 5 min. intervals in 2008 and 2009. In all three years the personal weather station was situated at the hide in the NSA. Rainfall data were collected in all three years using a simple conical rain gauge placed close to the hide. In 2008 and 2009 the personal weather station also collected rainfall data via a wireless rain sensor that gathered rainfall in a 'bucket seesaw mechanism' that tipped and recorded the volume of rainfall at 0.7 mm intervals. The rainfall data were collected on a daily cycle, where rainfall was recorded from the time the observer left the hide on day *x* to the time in which the observer left the hide on day *x*+1. Therefore, any rainfall that occurred overnight (from leaving the hide to returning to the hide the following day) contributed to the following days rainfall data. The Thermo-Hygro sensor for the personal weather station was placed in the shade. Hourly data from the Met Office weather station on North Rona were obtained from the British Atmospheric Data Centre (BADC) for the 2007 and 2008 breeding seasons; unfortunately this weather station was decommissioned shortly before the 2009 field season. Across all three years the personal weather station omitted data for several days, primarily due to technical errors and during one instance of very extreme weather on 25th October 2008 when the hide and the weather station were destroyed during storm force winds. Consequently, no weather data were collected by the personal weather station for the remainder of the 2008 field season.

The hourly weather data collected by the Met Office weather station at Sule Skerry (59° 05'N, 04° 24'W) were also obtained from BADC for the dates of the 2007, 2008 and 2009 field seasons on North Rona. Sule Skerry is a remote skerry in the North Atlantic, on a similar latitude to North Rona (59°06'N, 05° 50'W) and is approximately 75 km to the east of North Rona. The data from the Sule Skerry weather station were tested for collinearity between both personal weather stations and the Met Office weather station on North Rona. This was done to assess whether it would be possible to use the weather data collected at Sule Skerry for all three years. Although this would not provide a local, fine-scale

Figure 2.8: The following three plots present the correlations between the air temperature (^{o}C) data collected by the three weather stations: the North Rona Met Office weather station (NRWS), the Sule Skerry Met Office weather station (SSWS) and the personal weather station (PWS; DataHogg2) during the 2007 field season. The results of the Spearman's rank correlation coefficient are shown in the legend in the top left corner of each plot. The black solid line shows the line of best fit; the grey dashed line shows the 1:1 line.


n=176, r=0.8, p=<0.001
Air Temp °C (NRWS) 2007
Air Temp °C (PWS) 2007
6
7
8
9
10
11
12
6
8
10
12
14
16


n=176, r=0.75, p=<0.001
Air Temp °C (SSWS) 2007
Air Temp °C (PWS) 2007
7
8
9
10
11
12
13
6
8
10
12
14
16

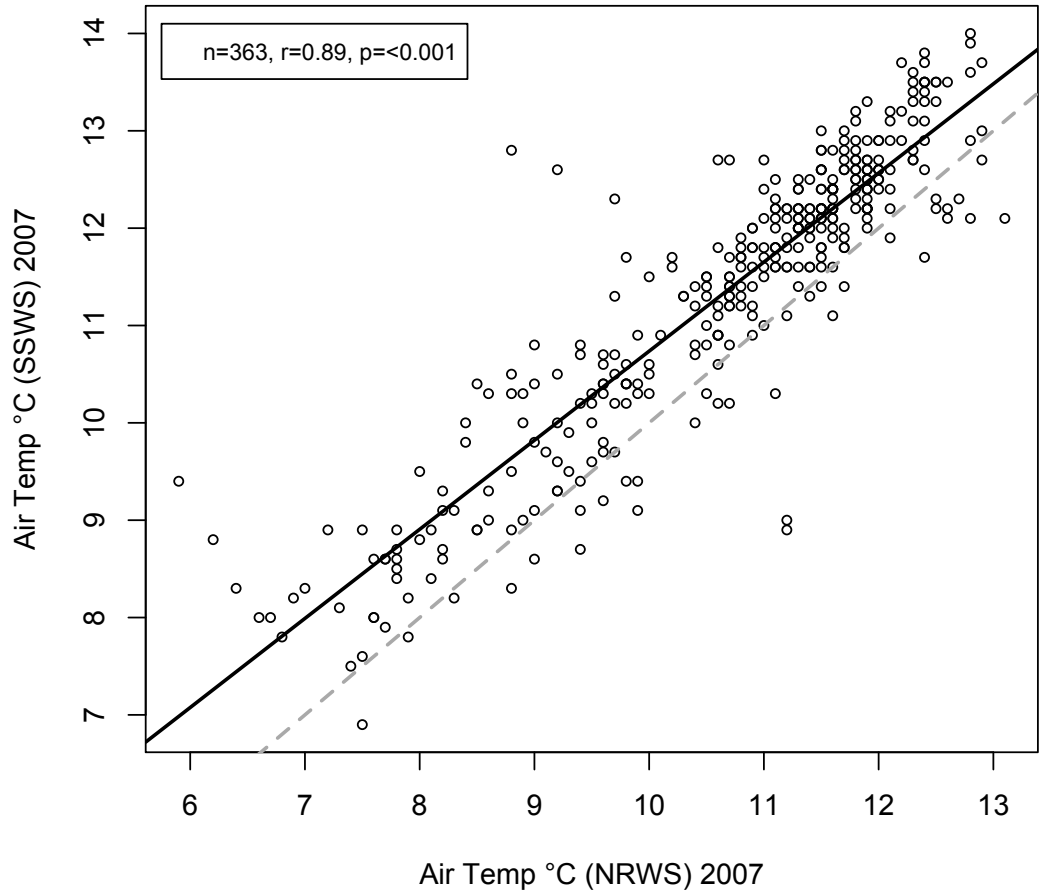
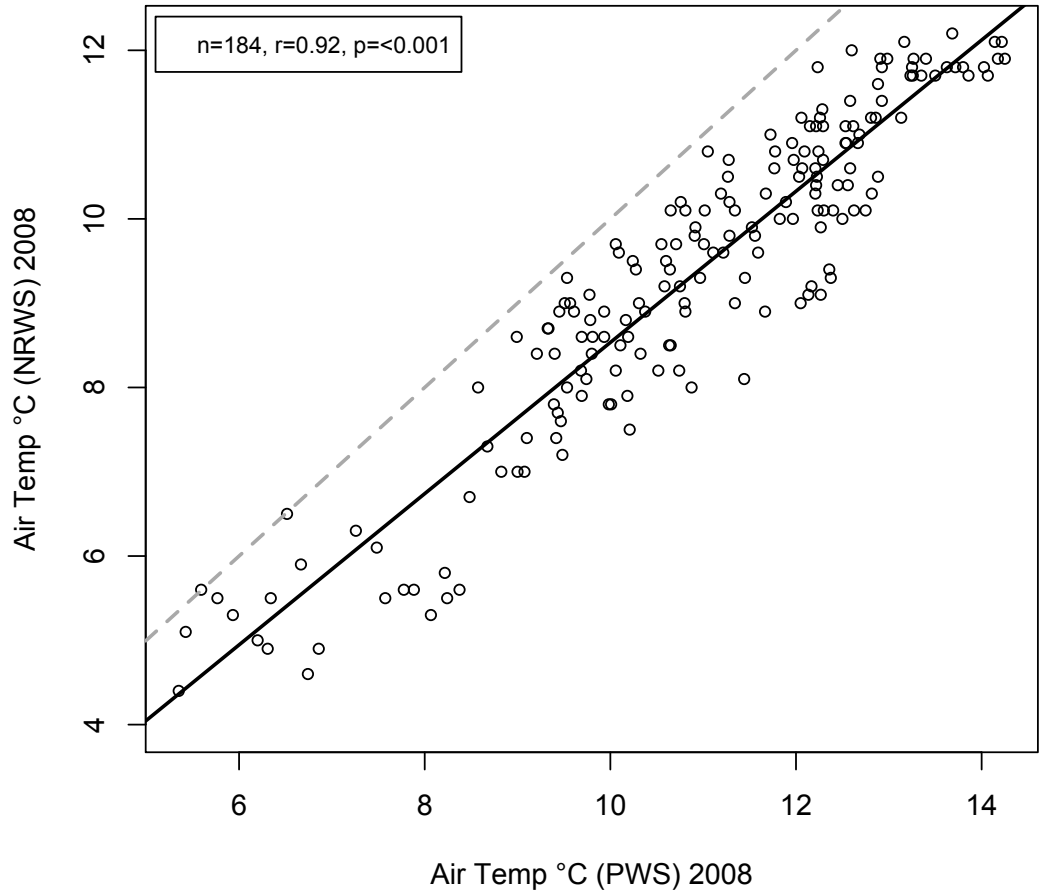
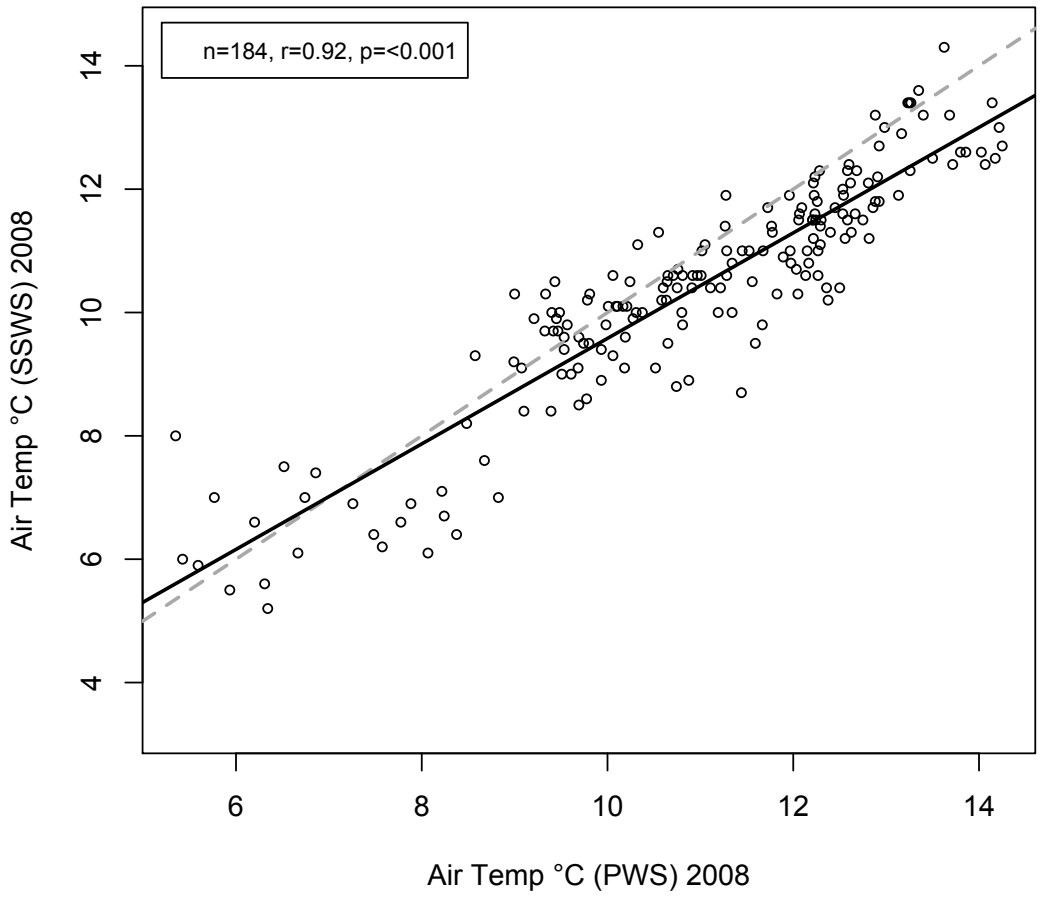
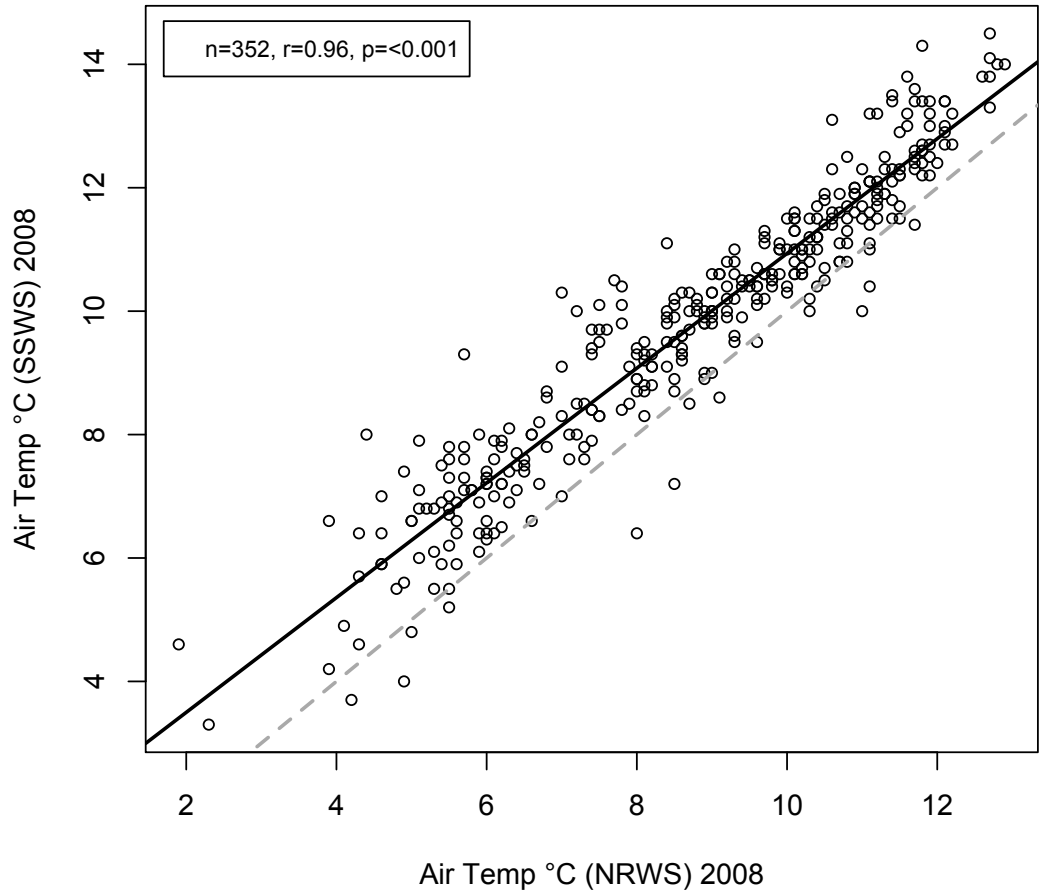

n=363, r=0.89, p=<0.001
Air Temp °C (SSWS) 2007
Air Temp °C (NRWS) 2007
7
8
9
10
11
12
13
14
6
7
8
9
10
11
12
13

Figure 2.9: The following three plots present the correlations between the air temperature data (^{o}C) collected by the three weather stations: the North Rona Met Office weather station (NRWS), the Sule Skerry Met Office weather station (SSWS) and the personal weather station (PWS; Nexus Professional Weather Station 35.1075) during the 2008 field season. The results of the Spearman's rank correlation coefficient are shown in the legend in the top left corner of each plot. The black solid line shows the line of best fit; the grey dashed line shows the 1:1 line.


n=184, r=0.92, p=<0.001
Air Temp °C (NRWS) 2008
Air Temp °C (PWS) 2008
4
6
8
10
12
6
8
10
12
14


n=184, r=0.92, p=<0.001
Air Temp °C (SSWS) 2008
Air Temp °C (PWS) 2008
4
6
8
10
12
14
6
8
10
12
14


n=352, r=0.96, p=<0.001
Air Temp °C (SSWS) 2008
Air Temp °C (NRWS) 2008
4
6
8
10
12
14
2
4
6
8
10
12

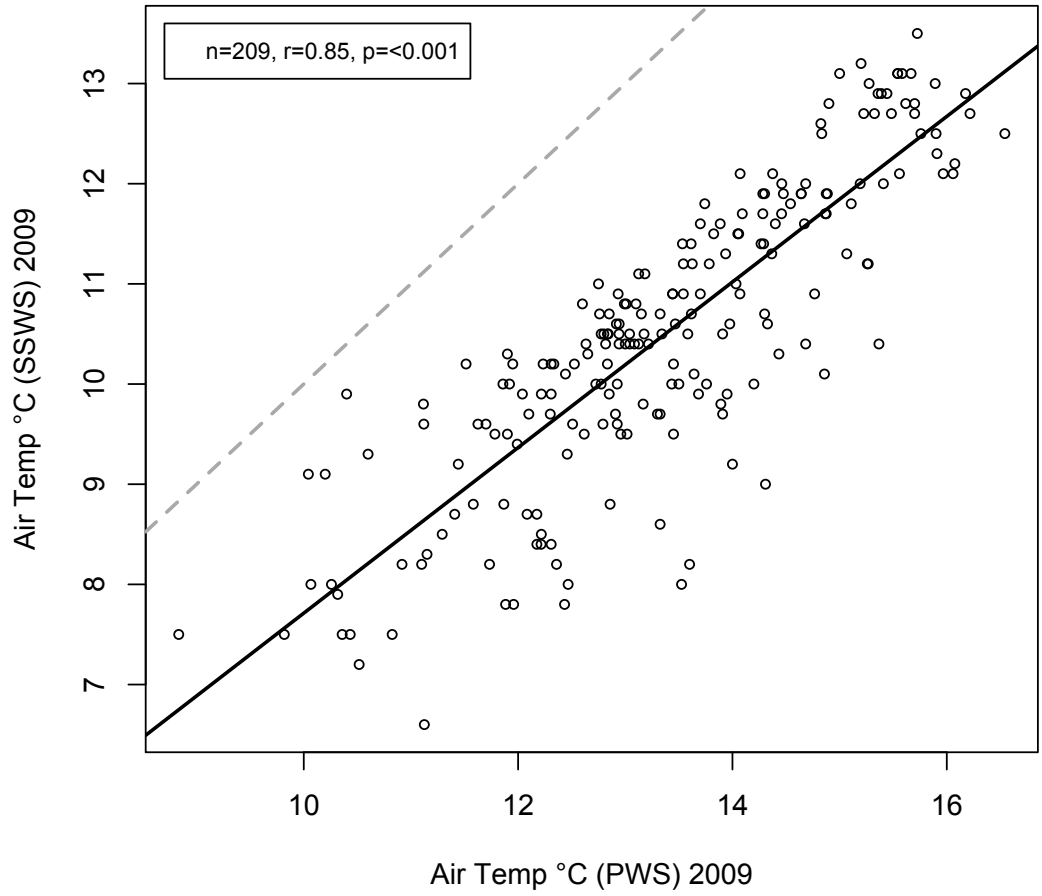
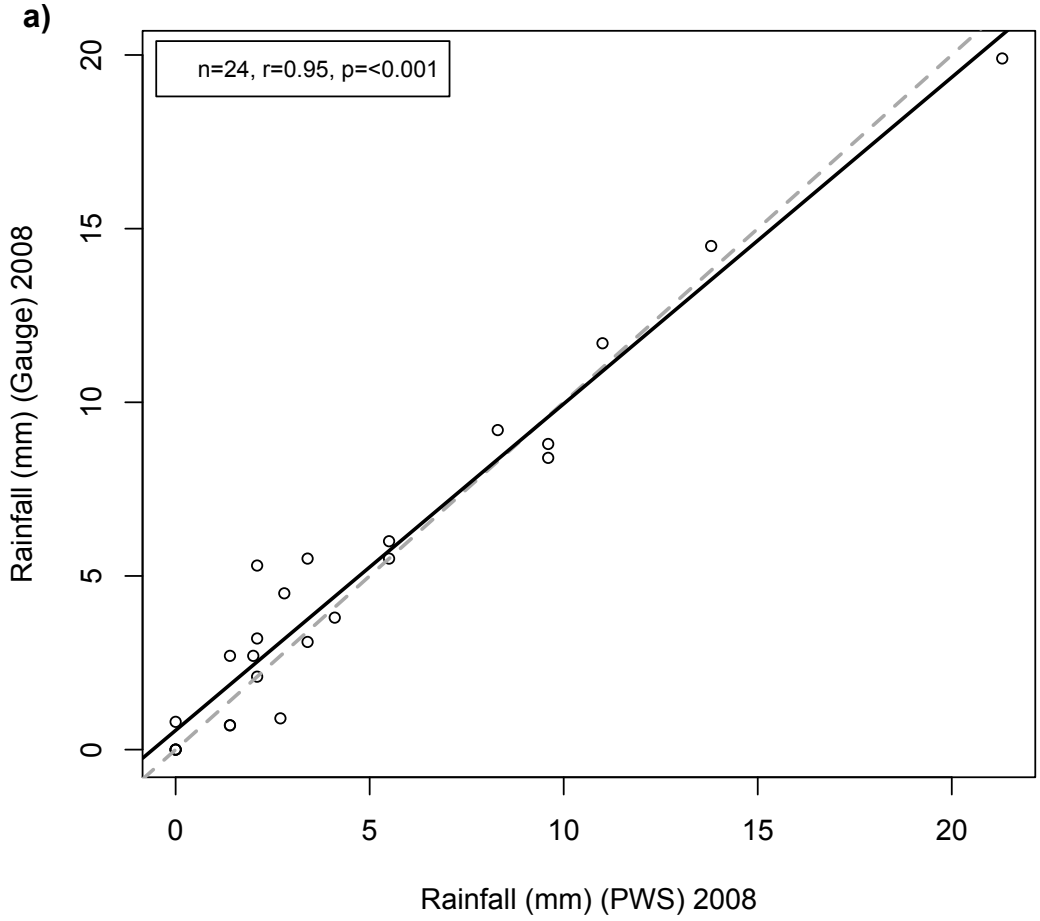
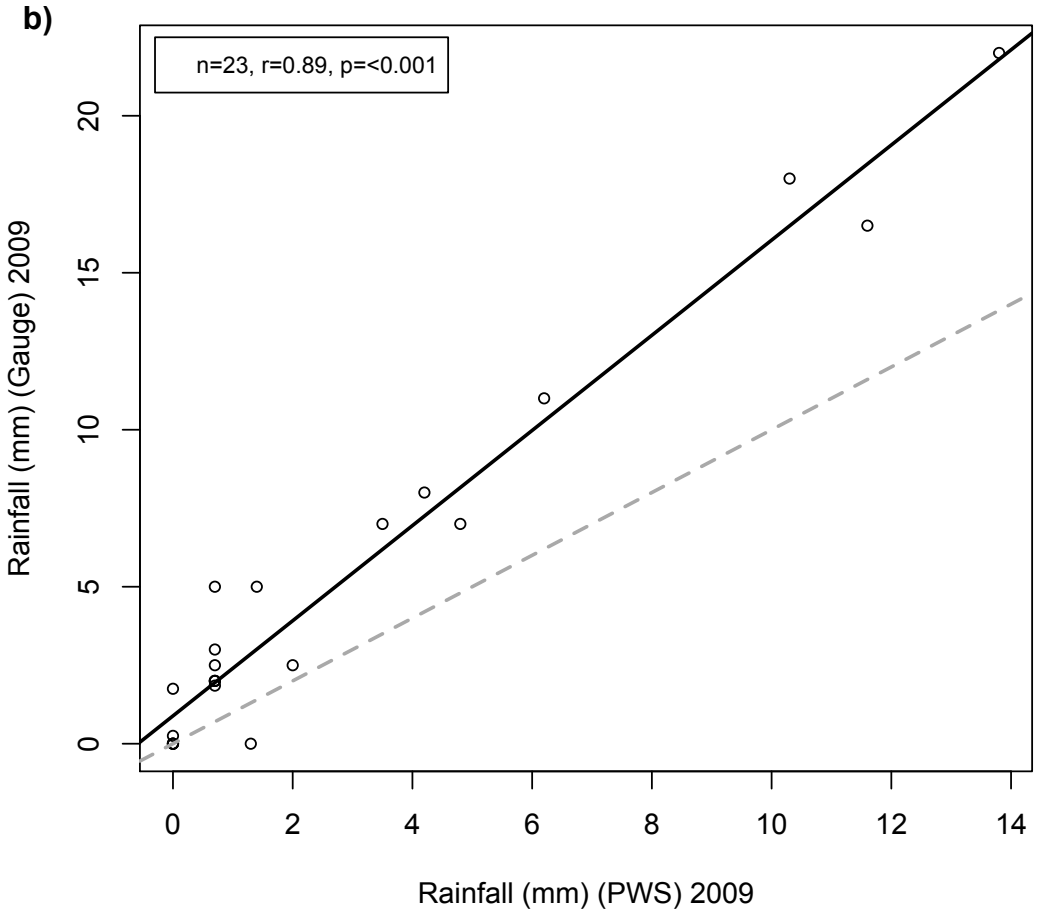


Figure 2.10: The correlation between the air temperature data (^{o}C) collected by the Sule Skerry Met Office weather station (SSWS) and the personal weather station (PWS; Nexus Professional Weather Station 35.1075) during the 2009 field season. The results of the Spearman's rank correlation coefficient are shown in the legend in the top left corner. The black solid line shows the line of best fit; the grey dashed line shows the 1:1 line.

Figure 2.11: The correlation between the rainfall data (mm) collected by the simple conical rain gauge ('Gauge') and the Personal Weather Station ('PWS'; Nexus Professional Weather Station 35.1075) during the (a) 2008 and (b) 2009 field seasons. The results of the Spearman's rank correlation coefficient are shown in the legend in the top left corner of each plot. The black solid line shows the line of best fit; the grey dashed line shows the 1:1 line.


a)
n=24, r=0.95, p=<0.001
Rainfall (mm) (Gauge) 2008
Rainfall (mm) (PWS) 2008
0
5
10
15
20


b)
n=23, r=0.89, p=<0.001
Rainfall (mm) (Gauge) 2009
Rainfall (mm) (PWS) 2009
0
2
4
6
8
10
12
14
5
15
20

measure of temperature, it would have the advantage of minimising data loss and keeping the measurement of air temperature constant across the three field seasons.

For each breeding season the hourly mean of the air temperature data recorded by the personal weather stations, and the hourly data for the North Rona and Sule Skerry Met Office weather stations were tested for collinearity (with the exception of the North Rona weather station in 2009). All of the air temperature measures were significantly collinear with one another (Figures 2.8 - 2.10). The correlation between the personal weather station and the Sule Skerry Met Office weather station were highly significant for all three years (**2007**, r = 0.75, $p < 0.001$, n = 176; **2008**, r = 0.92, $p < 0.001$, n = 184; **2009**, r = 0.85, $p < 0.001$, n = 209). In addition, the rainfall data from the personal weather station in 2008 and 2009 were significantly collinear with the simple conical rain gauge (**2008**, r = 0.95, $p < 0.001$, n = 24; **2009**, r = 0.89, $p < 0.001$, n = 23; Figure 2.11). Therefore, the air temperature data from Sule Skerry and the rainfall data from the simple conical rain gauge will be used in the analyses presented in the subsequent chapters.

2.5.8. Mother and pup variables

For the majority of the females in the NSA it was possible to gather accurate data on: 1) the day the female gave birth, 2) the day the female left the breeding colony, 3) the duration of the females' stay postpartum, 4) the age of the females' pup. If the date of birth of a females' pup was not known, the five stages of age class as described in Boyd et al. (1962) and Redman (2002) were used to estimate the age of the pup (Table 2.2; Figure 2.12). In 2007 and 2008 the stages of pups were noted in the field notebook regularly. In 2009 the stages of all the pups in the NSA were noted on the first map of the day (Figure 2.7). In the case of births that occurred between leaving the hide in the evening and returning the following morning the date of birth of the pup was recorded as the day before.

Pups were sexed opportunistically from the hide using binoculars. Where possible, individuals were sexed multiple times throughout lactation in order to increase the confidence in the observation. The pup was sexed based on the

location of the genital slit: for females, the genital slit is next to the anus and for the males it is approximately half way between the naval and anus. In the case of younger pups observing individuals urinating, or the location of fresh urine patches on the white pelage can help to identify the sex of an individual. For older pups, the loss of the thicker white pelage can make identification of the genital slit clearer.

Table 2.2: Descriptive age categories for grey seal pups (based on Boyd et al. 1962, Boyd & Campbell, 1971 and Redman, 2002). The approximate age of the pup is based on qualitative observations over the three field seasons.

Age class	Approx. Age (Days)	Description
Stage I (Figure 2.12a)	1-3	Pup lacks co-ordination and the contours of the ribs, hips and shoulders are clearly visible. The umbilicus looks pink and fresh and the skin forms loose folds around the neck and shoulders; there may be a yellowish tint to the pelage.
Stage II (Figure 2.12b)	4-8	Pup shows improved co-ordination and the ribs become less prominent as a layer of blubber is deposited. The umbilicus is dried and shrivelled (it is lost in the early part of this stage) and the pelage is white.
Stage III (Figure 2.12c)	8-14	Pup shows good co-ordination and the body is barrel-shaped. The pelage is white, although the muzzle and flippers may show a slight loss of natal coat. There are no signs, on the body, of moulting to the juvenile pelage.
Stage IV (Figure 2.12d)	14-17	Pup starts moulting to the juvenile pelage, although the white coat is still present in places.
Stage V (Figure 2.12e)	18+	Pup is completely moulted to the juvenile pelage.

Figure 12a: Stage I

Figure 12b: Stage II

Figure 12c: Stage III

Figure 12d: Stage IV

Figure 12e: Stage V

Figure 12: Photographs of pups showing the five stages used to describe the age of a pup. These photographs correspond to the descriptions given in Table 2.2.

Chapter Three:
Exploratory data analysis

3.1. Introduction

Data exploration is often regarded as a very important prerequisite before the desired analysis is undertaken. Yet, in many cases this technique is often overlooked, or at best, little information is given on how the exploratory analyses were carried out (Zuur et al., 2009a). In this chapter, thorough data exploration of the dataset containing all postpartum females for all three years combined (2007 - 2009) is carried out. This dataset will hereafter be referred to as the gross dataset. The analyses presented in the following chapters were carried out using datasets that only included individuals that were re-sighted in two or more breeding seasons. The latter sections of this chapter will present a detailed exploratory analysis of these datasets, which shall hereafter be referred to as the re-sighted individuals' datasets.

Where relevant, the protocol for data exploration proposed by Zuur et al. (2009a) was followed, this included:

1) Identifying and dealing with outliers.
2) Checking for collinearity between explanatory variables.
3) Assessing whether the dataset is zero inflated.
4) Checking for independence.

An explanatory variable is a variable that will be used to explain or predict the response variable (a behavioural category); this term is considered synonymous with covariate. For the gross behavioural and spatial data non-parametric summary statistics were used in order to give less weight to potential outliers.

Given the structure of this chapter, it is often necessary to discuss the results of the exploratory analyses before proceeding to the next step in the analytical process. Without discussing the results as this chapter progresses, it would not be possible to explain or justify the subsequent approaches. For this

reason, this chapter takes an unorthodox approach of briefly discussing the results at each stage of the analyses, rather then revisiting the analyses at the end of the chapter, where discussion of some results may seem somewhat redundant.

3.2. Pseudoreplication of re-sighted individuals

The initial number of individuals in the gross dataset prior to the exploratory analyses was 123. These data will be referred to as individuals; however, given that 19 individuals were re-sighted in two or more breeding seasons, *actual* individuals may be recorded up to three times. To avoid any confusion when making reference to individuals and re-sighted individuals the former shall be referred to using 'n' (n = 123) and the latter shall be referred to using 'N' (N = 19). Since re-sighed individuals are not independent observations these data are prone to pseudoreplication (Hurlbert, 1984). The method used to avoid pseudoreplication varied depending on the statistical analyses undertaken. These methods are detailed in the relevant sections within this chapter and subsequent chapters. Dealing with pseduoreplication was only deemed necessary if reliable *p* values from the subsequent statistical tests were required (Hurlbert, 1984; Heffner et al., 1996).

3.3. Data transformation

There are many opinions in the literature regarding data transformation and when it should be used. The commonly cited reasons for using transformation techniques are to reduce the effects of outliers, to stabilise the variance and to linearise relationships (Fowler et al., 1998). However, some authors argue that making predictions using transformed data can be difficult because of the complex back transformations that are required in order to obtain a true value (Zuur et al., 2009a, b). Where the response variable is proportional (as is the case in the current study; i.e. the proportion of time an individual spent performing a given behaviour), it has been argued that an arcsine transformation should be used because these data are strictly bounded (i.e. the percentage of time in a given behaviour cannot be greater than 100% nor can it be less than 0%; Fowler et al., 1998; Zar, 1998).

The majority of references that are commonly cited as a reason for arcsine transforming proportional data are generally more than a decade old (Fowler et al., 1998; Zar, 1998). More recently, Warton & Hui (2011) revisited whether or not there is still a need to arcsine transform proportional data. They found that for binomial data, logistic regression had greater interpretability and higher power than the analyses of the transformed data. Their findings support the opinion of a growing number of researchers that believe that the advances in ecological statistics has resulted in classical approaches being superseded by more effective analytical approaches, such as logistic regression and generalised linear mixed models (GLMMs; Bolker, 2008; Bolker et al., 2009; Zuur et al., 2009b; Richards et al., 2011; Warton & Hui, 2011). As a consequence, these researchers advocate the use of statistical approaches that suit a particular dataset, rather than transforming data to suit classical statistical frameworks. Therefore, in the current study a more appropriate analysis will be favoured in order to avoid the transformation of the response or the explanatory variables.

3.4. Gross activity plots

The initial stage in the analyses of the gross behavioural data was to assess the minimum number of scan samples required from an individual in order to obtain an accurate representation of a postpartum female grey seal's activity whilst on the breeding colony. To do this, the percentage of time spent in each behavioural category was plotted against the sample size for each individual; these plots shall be referred to as gross activity plots (Figure 3.1). There is a clear pattern for the resting behavioural category, which shows that smaller sample sizes result in estimates of less time spent resting. Consequently, given that resting comprises the majority of an individual's activity budget, it is likely that individuals with lower sample sizes will have an over-estimated percentage of time spent in one or more of the other behavioural categories. Twiss (1991) reported a similar pattern in the resting behaviour of male grey seals, and consequently applied a cut-off of 180 scan samples. In the case of females in the present study, it was decided, based on the gross activity plots, that a slightly higher cut-off of 200 scan samples should be applied to all eight of the behavioural categories (Figure 3.1). Applying this cut-off reduced the number of individuals in the gross

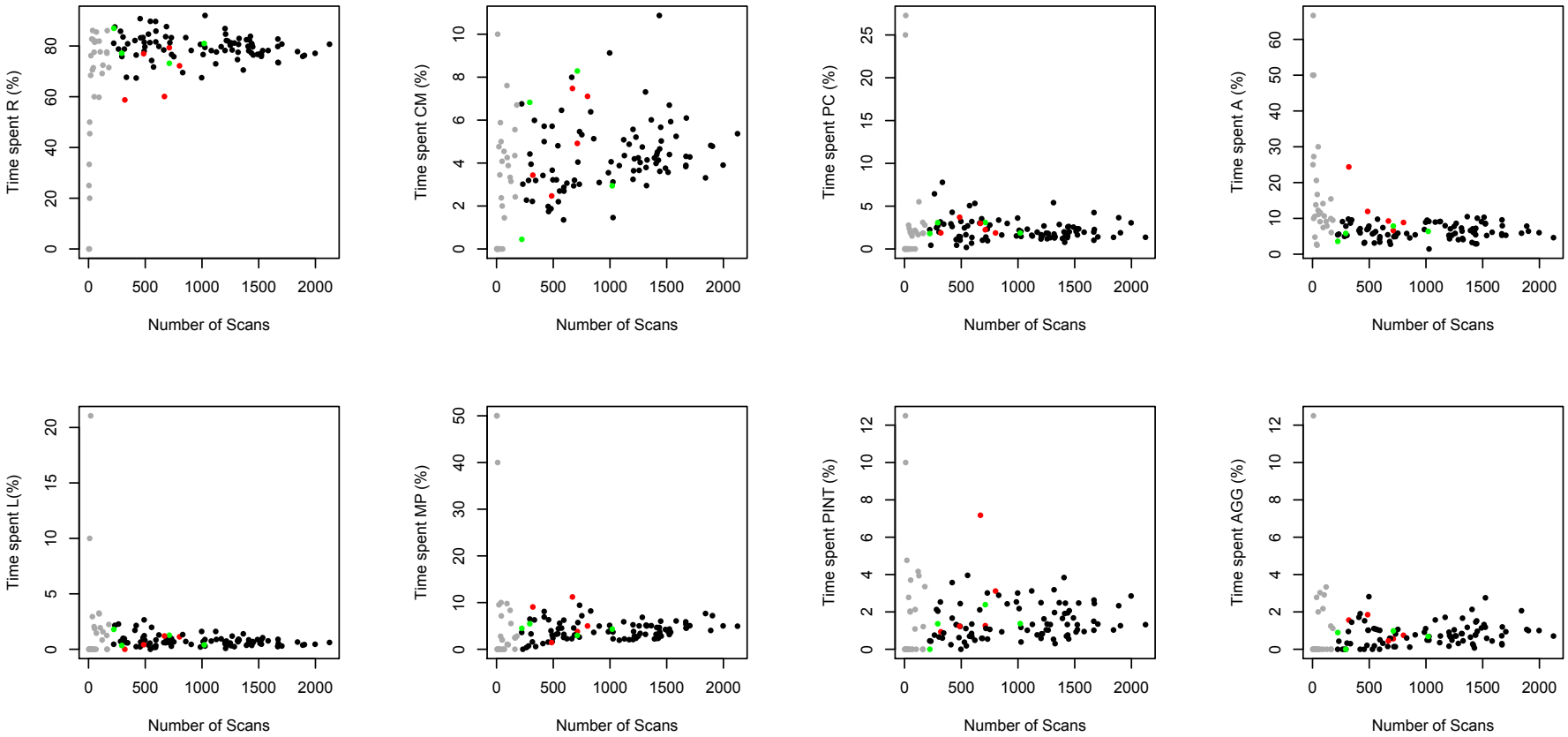


Figure 3.1: The gross activity plots for the resting (R) comfort movement (CM) pup check (PC) alert (A) locomotion (L) presenting & nursing (MP) pup interactions (PINT) aggression (AGG) behavioural categories for all individuals (n = 123) for all 3 years combined (2007 - 2009). The individuals with < 200 scan samples are shown in dark grey, the 5 additional individuals that were omitted from the dataset based on in-field observations are shown in red and the 4 additional individuals that were omitted from the dataset based on the spatial data are shown in green. The black data points show the individuals (n = 86) that were retained in the gross dataset.

dataset from 123 to 95. As a result, there is no clear trend relating to the number of scan samples collected for any of the eight behavioural categories. However, of those individuals with ≥ 200 scan samples it is clear that there is a lot of individual variation in the percentage of time a female spends in each of the behavioural categories (Figure 3.1).

3.4.1. Addressing outliers in the gross activity plots

The principal approach used to address potential outliers was to investigate the percentage of time an individual spent out-of-sight and to consult *ad libitum* notes taken in the field. Using this approach an additional five females were omitted from the dataset; these data points are shown in Figure 3.1. The reason each of these females were omitted is as follows: two of the females spent more than 50% of their time out-of-sight; the third female was positioned near a steep gully, and because of her location it was often difficult to observe her behaviour; the fourth female may not have been the same individual throughout (there were limited opportunities to obtain suitable photo-identification photographs, primarily due to poor weather conditions and the distance this individual was from the hide); the fifth female abandoned her pup after 11 days postpartum and began to nurse a neighbouring pup. She was discarded from the analyses in case she displayed any atypical behaviour preceding or following the event. In the case of the first two females it is likely, based on the data and the field notes, that they were primarily resting out-of-sight in pools that were not visible from the hide, which would explain the decreased percentage of time spent resting compared to the other individuals. Incidentally, despite the majority of individuals spending a percentage of time out-of-sight (Table 3.1; median = 0.60%; Inter-quartile range = 2.02%) there was no indication that any other individuals should be omitted from the gross dataset purely on this basis alone.

There were four additional individuals omitted from the gross dataset as a result of the exploratory analyses of the spatial data (see Section 3.8.1, for more details). Therefore, in order to maintain consistency with respect to which individuals were included in the analyses presented in this chapter, these four

individuals were omitted from the gross dataset (n = 86) prior to the analyses of the gross behavioural data.

3.5. Gross activity budget

Table 3.1 and Figure 3.2 present the summary statistics for the gross activity budget for the 86 postpartum females. There are indications from Figure 3.2 that outliers may still be present in the dataset. However, it is important to note that not all data points that are out-with the lower and upper quartiles in a boxplot should be considered as outliers and removed (Zuur et al., 2009a). Caution when removing outliers is of great importance, particularly in this instance when the ultimate questions being addressed relate to individual variation in behaviour. Therefore, it is important not to mistake individual variation as an erroneous data point.

Table 3.1: The non-parametric summary statistics for the gross percentage of time spent in each of the nine behavioural categories (including the sex behavioural category) for the postpartum females (n = 86) for all three years (2007 - 2009) combined. Summary statistics for the percentage of time spent out-of-sight and for the number of scan samples per individual are given in the penultimate and last row, respectively.

Behaviour	Median	IQR	Min.	Max.
Resting	79.76	5.56	67.38	92.02
Comfort move	4.1	1.9	1.35	10.87
Pup check	1.97	1.29	0.18	7.78
Alert	6.04	2.63	1.46	10.48
Locomotion	0.65	0.44	0	2.65
Presenting & nursing	3.79	2.45	0	9.43
Pup interactions	1.28	1.36	0	3.96
Aggression	0.72	0.75	0	2.82
Sex	0.12	0.59	0	2.22
Out-of-sight*	0.60	2.02	0	37.7
Scan samples	***1102***	***865***	***222***	***2124***

*Note that the data for the nine behavioural categories displayed here were calculated excluding out-of-sight records. The summary data presented for out-of-sight was calculated in a separate analysis.

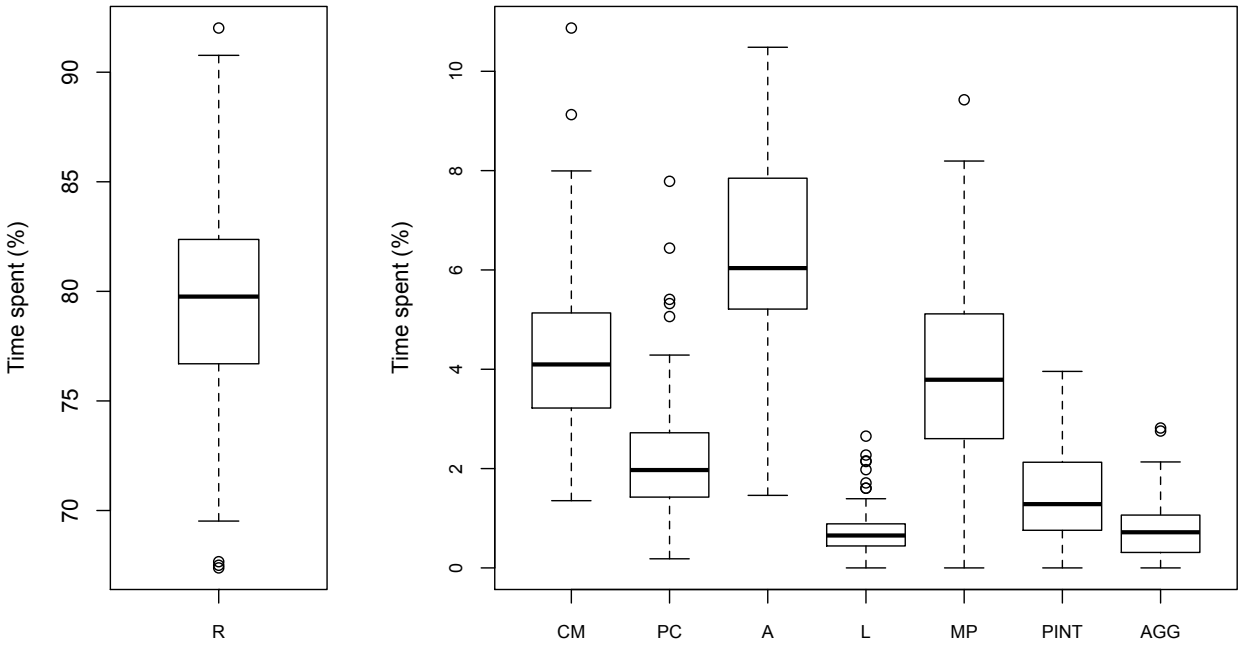


Figure 3.2: The gross behavioural data for the postpartum females (n = 86) over the three years (2007 - 2009) combined for the resting (R), comfort movement (CM), pup check (PC), alert (A), locomotion (L), presenting & nursing (MP), pup interactions (PINT) and aggression (AGG) behavioural categories. The percentage of time spent resting is considerably greater than that on the other 7 behavioural categories; therefore, it is presented in a separate plot. The summary statistics for these data are shown in Table 3.1.

On average, postpartum female grey seals spent ca. 80% of their time resting (Table 3.1; median = 79.76%), which is comparable to previous studies on U.K. grey seal breeding colonies (Anderson & Harwood, 1985). This leaves little time for the other eight behavioural categories (including the sex behavioural category, which although not included in the subsequent analyses does account for a percentage of the activity budget; Table 3.1; Chapter 2, Section 2.5.3). This is reflected in the fact that several behaviours have a minimum value of 0%, which is unlikely to be a true reflection of an individual's behaviour. However, this may well be an effect of the sampling protocol, which has already been discussed in Chapter 2, Section 2.5.4.

3.6. Lactation period analyses of the behavioural data

In the early stages of lactation the probability of pup mortality is much greater in the first few days postpartum (Coulson & Hickling, 1964) with the largest cause of mortality resulting from the mother-pup bond either not forming or being broken (Anderson et al., 1979). In the later stages of lactation, at approximately day 16, the mother comes into oestrus (Pomeroy et al., 1999; Twiss et al., 2006). This represents the point of transition between maternal care and the quick process of mating, weaning the pup, and leaving the colony (Chapter 2; Section 2.2.1).

To assess whether there were any significant differences in behaviour during the time spent on the colony postpartum, the behavioural categories were divided into three lactation periods. These were defined as: 1) early lactation; the pup was less than 4 days old, 2) mid lactation; the pup was between 4 and 15 days old, 3) late lactation; the pup was ≥ 16 days old. If the age of the pup was not known it was estimated using the guidelines discussed by Boyd et al. (1962) and Redman (2002) (Chapter 2, Section 2.5.8). Furthermore, although every effort was made to gather data for every known female for every day postpartum this was not always possible, with the missing data typically occurring during early and late lactation (Tables A3.1 - A3.3). The main reasons for missing data were: 1) missing the birth of the pup, 2) the field team leaving the colony before the female departs, 3) assisting in other field studies, 4) unsafe weather conditions preventing observation, 5) the female was out of sight for extended periods of time.

Given the relatively small sample size of individuals, Kruskal-Wallis tests were used to assess whether there was a significant difference between the lactation periods for each of the eight behavioural categories. A *post hoc*, multiple comparison test as discussed by Siegel & Castellan (1988; pp 213 - 214) was used to identify which of the lactation periods were significantly different from one another. To avoid pseudoreplication the percentage of time spent in a behavioural category by a re-sighted individual was calculated using the data from all of the breeding seasons in which that individual was seen (Crawley, 2007). This resulted

in a sample size of 61 individuals. The multiple comparison tests were carried out using the kruskalmc() function in the R package *PIGRMESS* (Giraudoux, 2011).

Table 3.2: The results of the Kruskal-Wallis tests and the *post hoc* multiple comparison tests for the percentage of time spent in each behavioural category during each of the three lactation periods (LP) for all females (n = 61) (LP1 n = 56; LP2 n = 59; LP3 n = 53) for all three years (2007 - 2009) combined. Significant results are in bold. The *post hoc* analyses show the observed (Obs.) and critical (Crit.) values (d.f. = 2). The full name of each of the behavioural categories is shown in the footnote.

			LP1 - LP2		LP1 - LP3		LP2 - LP3	
Behaviour	Chi-Sq	*p*	Obs.	Crit.	Obs.	Crit.	Obs.	Crit.
R	**6.69**	**0.04**	5.15	21.72	**23.02**	**22.32**	17.87	22.04
CM	4.25	0.12	1.93	21.72	15.56	22.32	17.49	22.04
PC	**9.68**	**0.008**	3.41	21.72	**26.68**	**22.32**	**23.27**	**22.04**
A	3.46	0.18	13.27	21.72	16.11	22.32	2.84	22.04
L	**20.37**	**<0.001**	10.12	21.72	**40.3**	**22.32**	**30.17**	**22.04**
MP	**38.23**	**<0.001**	**36.63**	**21.72**	**56.61**	**22.32**	19.98	22.04
PINT	**16.75**	**<0.001**	**33.02**	**21.72**	**31.85**	**22.32**	1.17	22.04
AGG	2.68	0.26	14.65	21.72	6.7	22.32	7.95	22.04

R = resting; CM = comfort movement; PC = pup check; A = alert; L = locomotion; MP = presenting & nursing; PINT = pup interactions; AGG = aggression

The results of the Kruskal-Wallis tests and the multiple comparison tests showed that there were significant differences between the lactation periods for the percentage of time spent in the resting, pup check, locomotion, presenting & nursing and pup interactions behavioural categories (Table 3.2). Certain behaviours do show clear patterns (Figure 3.3), such as the time spent presenting & nursing, which increased with lactation period, whilst the time spent in the pup check and locomotion behavioural categories decreased with lactation period. The pattern in the presenting & nursing behavioural category contradicts the findings of Iverson et al. (1993) who found that the daily intake of milk by pups on Sable

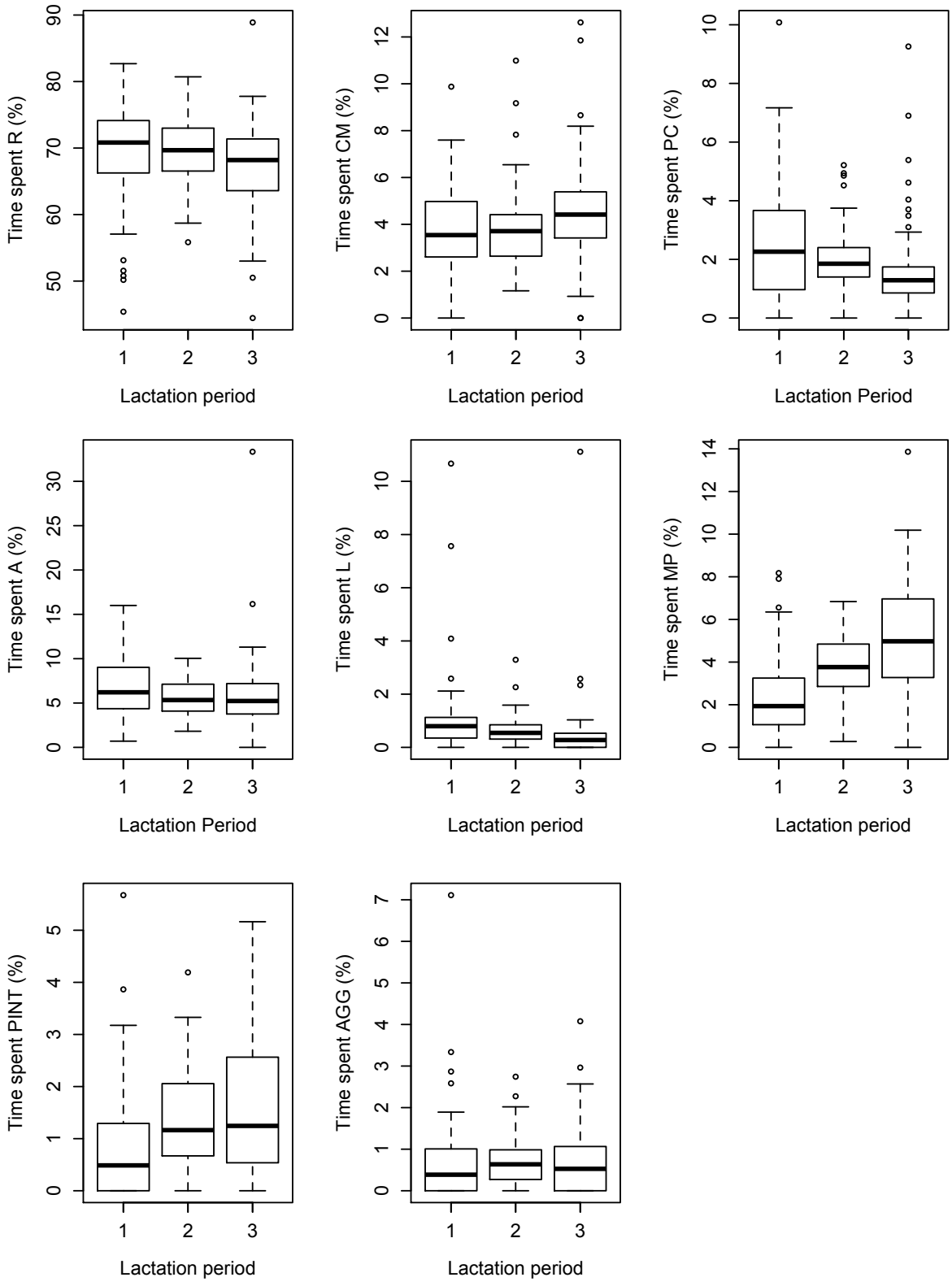


Figure 3.3: The lactation period (1 = early; 2 = mid; 3 = late) analyses for the resting (R), comfort movement (CM), pup check (PC), alert (A), locomotion (L), presenting & nursing (MP), pup interactions (PINT) and aggression (AGG) behavioural categories for the postpartum females (n = 61) for all three years (2007 - 2009) combined. The statistical analyses of these data are shown in Table 3.2.

Island (Nova Scotia, Canada) did not change during lactation. They reported that the increase in growth rate of the pup was due to an increase in the level of energy in the milk produced by the mother as the age of the pup increased. This would suggest that from a behavioural perspective the percentage of time spent presenting and nursing would be similar across lactation periods, yet that was not what was found in the present study. Other observational studies have reported varied patterns in presenting & nursing, where some have suggested that there is no change in the frequency as the pup grows (Fogden, 1971), whilst others have recorded a peak in the time spent presenting & nursing during the middle of lactation (Kovacs, 1987). The pattern in the locomotion behavioural category, reported in the present study has also been noted by Boness & James (1979), who found that as females enter oestrus the extent of their movement tended to decline. The principal aim of these analyses was to identify any gross variation in behaviour across the lactation periods that may assist in data selection for subsequent analyses. Therefore, outliers in these data are not investigated further.

3.7. Investigating temporal trends in the behavioural data

The behavioural data were checked for seasonal (day-to-day), diurnal (hour-to-hour) and pup age (days postpartum) patterns. All of the plots presented in this section show the mean and the 95% confidence intervals. The mean was preferred over the median because, with the exception of the resting behavioural category, the occurrence of behaviours were often very low, which made a considerable number of the median values for these behaviours 0, or close to 0. To obtain the 95% confidence intervals the data were bootstrapped. This was done using sampling with replacement, which draws an observation at random from the dataset and then returns the observation before drawing another random sample (Crawley, 2007). This was done using 10,000 replicates. The bootstrap resampling was carried out using the boot() function in the R package *boot* (Davidson & Hinkley, 1997; Canty & Ripley, 2011) and the 95% confidence intervals were extracted using the boot.ci() function, which is available in the same package. The 95% confidence intervals were plotted using the plotCI() function in the R package *gplots* (Warnes, 2011).

3.7.1. Seasonal analyses

The date of the first day of data collection was 30th September for all three years whilst the final date of data collection was 1st November in 2007 and 2009 and 31st October in 2008 (Chapter 2, Section 2.4). On rare occasions, data were not collected for an entire day. This was primarily due to assisting in other field studies or unsafe weather conditions (Tables A3.1 - A3.3). There were no clear patterns in the seasonal data (Figure 3.4); however, there was a greater degree of variation in the percentage of time spent in some of the behavioural categories during the first few days of data collection. This is likely to be a result of fewer females being present on the colony during the initial stages of the breeding season (Figure 3.4).

3.7.2. Diurnal analyses

All data were collected during daylight hours; however, as the breeding season progressed the daylight hours became fewer. Consequently, there were fewer scan samples collected between the hours of 08:00 - 09:00 and 18:00 - 19:00 (Figure 3.5). As noted above, there were days where data were not collected for the entire day. This was primarily due to assisting in other field studies during the morning and early afternoon (Chapter 2, Section 2.3.1), which is reflected in the lower number of scan samples collected during the earlier hours of the day.

Some of the behavioural categories did show clear diurnal patterns (Figure 3.5). For example, the percentage of time spent resting was at its lowest for the first hour of the day. Thereafter, time spent in this behaviour increased until it plateaued at approximately 11:00. This shift in the activity budget was primarily accounted for by the greater percentage of time spent alert during these earlier hours. Similar diurnal patterns of alert behaviour, whereby individuals are more alert at first light, have been shown in male grey seals too (Anderson, 1978). Other behavioural categories such as comfort movement and pup check also showed a peak in the earlier hours of the day. Of the remaining behavioural categories,

aggression showed a unique pattern, where the percentage of time spent dipped at approximately midday to early afternoon.

3.7.3. Pup age analyses

The pup age data were used to assess fine-scale temporal changes in behaviour over the course of lactation. This is in contrast to the lactation period analyses, which were used to identify gross changes in behaviour over coarse, but biologically meaningful time periods during lactation. At approximately day 18 postpartum, the number of females that had yet to wean their pup and leave the colony showed a considerable decline (Figure 3.6). Consequently, there is a lot of variation in the data beyond day 18 where sample sizes were lower (Figure 3.6). Nevertheless, there were patterns in some of the behavioural categories, for example, the percentage of time spent in the pup check behavioural category gradually decreased over the course of lactation, which is particularly evident towards mid and late lactation. Conversely, the percentage of time spent in the presenting & nursing and pup interactions behavioural categories increased gradually over the course of lactation. Unsurprisingly, the temporally fine-scale patterns shown in these plots mirror those of the more temporally coarse lactation period plots (Figure 3.3).

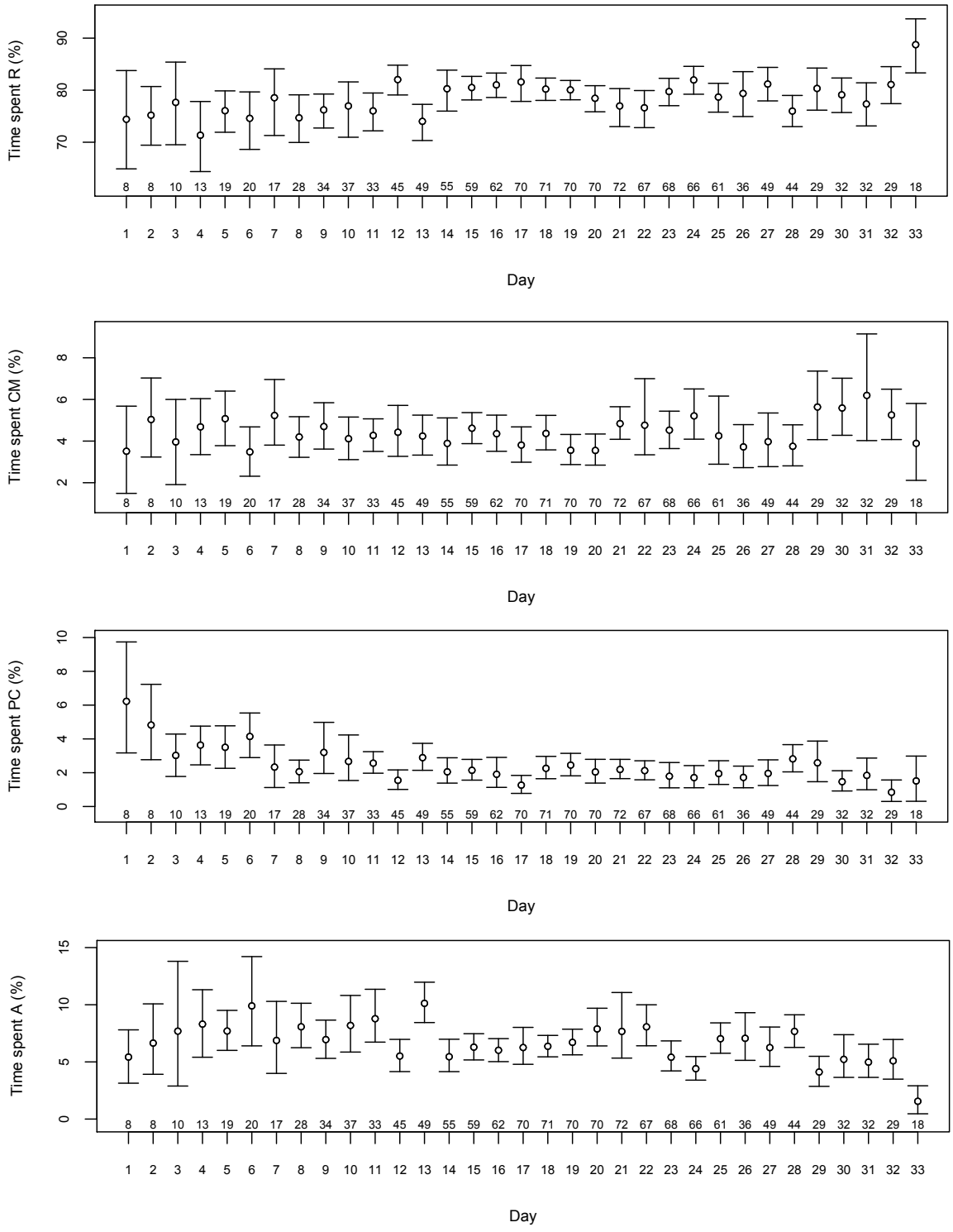


Figure 3.4: The seasonal data for the percentage of time spent in each of the eight behavioural categories: resting (R), comfort movement (CM), pup check (PC) alert (A) locomotion (L) presenting & nursing (MP) pup interactions (PINT) aggression (AGG). Day 1 = 30th September. On the x-axis, within the plot, the total number of individuals that comprise the sample for each of the days is shown. The plots are continued over the page.

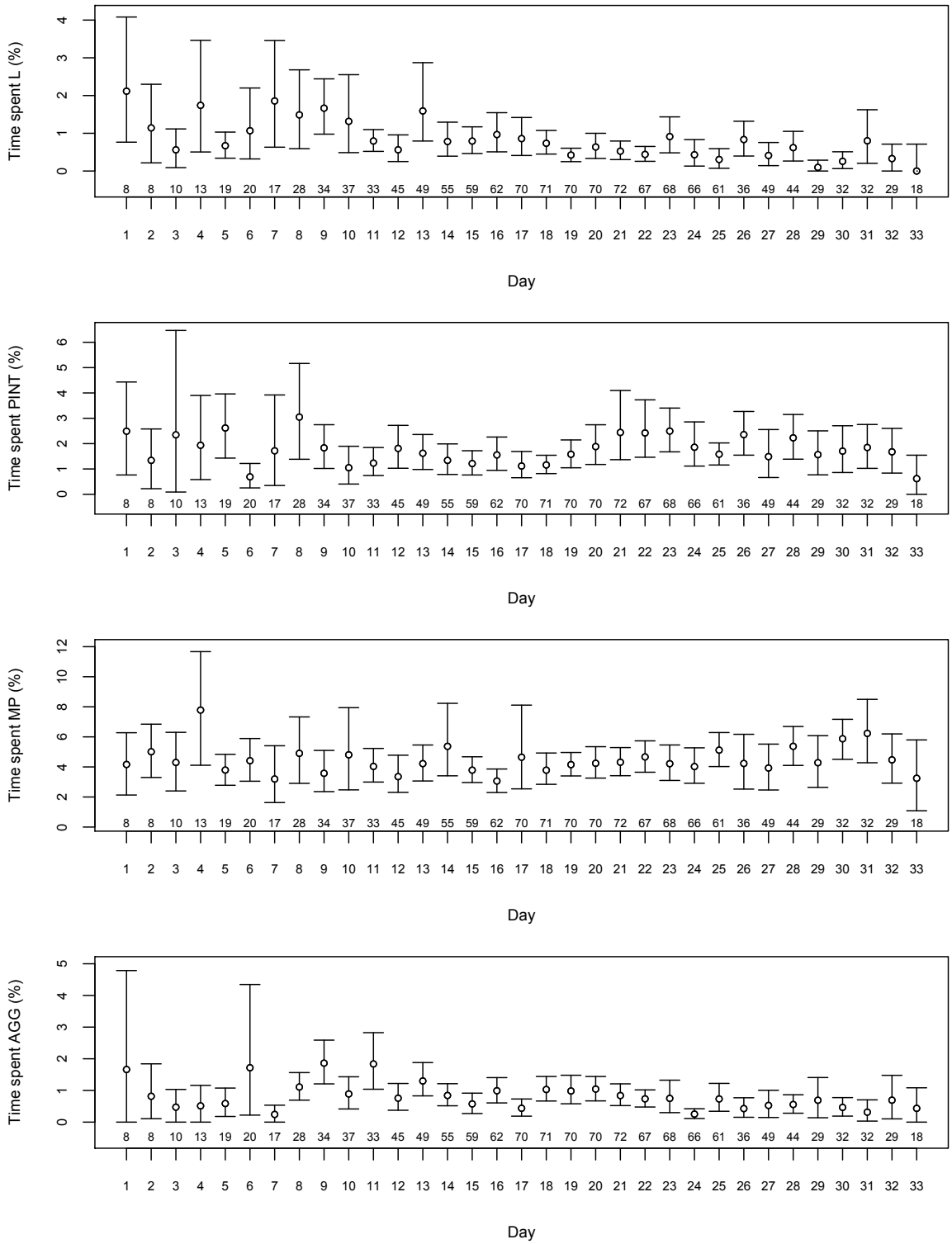
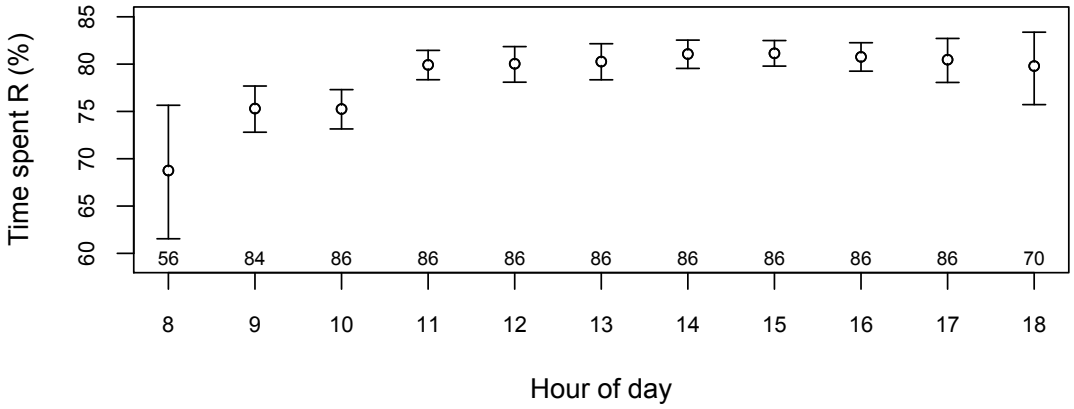

Time spent L (%)
0 1 2 3 4
8 8 10 13 19 20 17 28 34 37 33 45 49 55 59 62 70 71 70 70 72 67 68 66 61 36 49 44 29 32 32 29 18
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33
Day
Time spent PINT (%)
0 1 2 3 4 5 6
8 8 10 13 19 20 17 28 34 37 33 45 49 55 59 62 70 71 70 70 72 67 68 66 61 36 49 44 29 32 32 29 18
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33
Day
Time spent MP (%)
0 2 4 6 8 10 12
8 8 10 13 19 20 17 28 34 37 33 45 49 55 59 62 70 71 70 70 72 67 68 66 61 36 49 44 29 32 32 29 18
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33
Day
Time spent AGG (%)
0 1 2 3 4 5
8 8 10 13 19 20 17 28 34 37 33 45 49 55 59 62 70 71 70 70 72 67 68 66 61 36 49 44 29 32 32 29 18
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33
Day

Figure 3.5: The following eight plots over the next two pages show the diurnal data for the percentage of time spent in each of the eight behavioural categories: resting (R), comfort movement (CM), pup check (PC) alert (A) locomotion (L) presenting & nursing (MP) pup interactions (PINT) aggression (AGG). The hour of the day (BST) is shown on the x-axis (i.e. 13 = 13:00); the data are divided such that data recorded between 13:00 - 13:59 are included in 13. On the x-axis, within the plot, the total number of individuals that comprise the sample for each of the hours is shown; the number of days in which samples were gathered for each of the hours (08:00 - 18:00) over the three breeding seasons was 25, 50, 63, 65, 69, 74, 84, 87, 85, 78, 41, respectively.


Time spent R (%)
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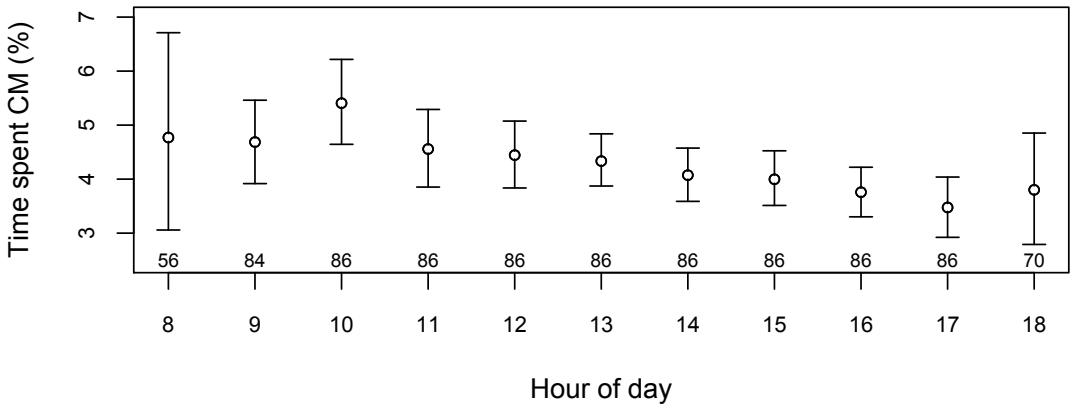
Hour of day


Time spent CM (%)
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7
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86
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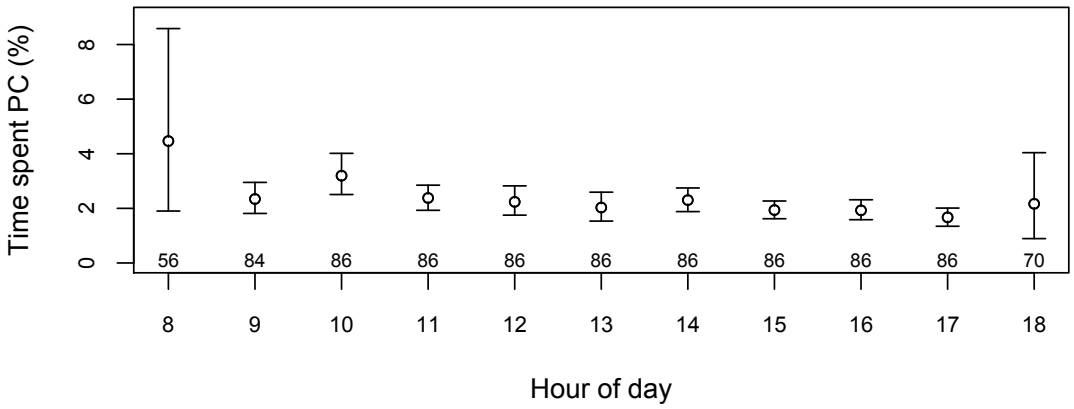
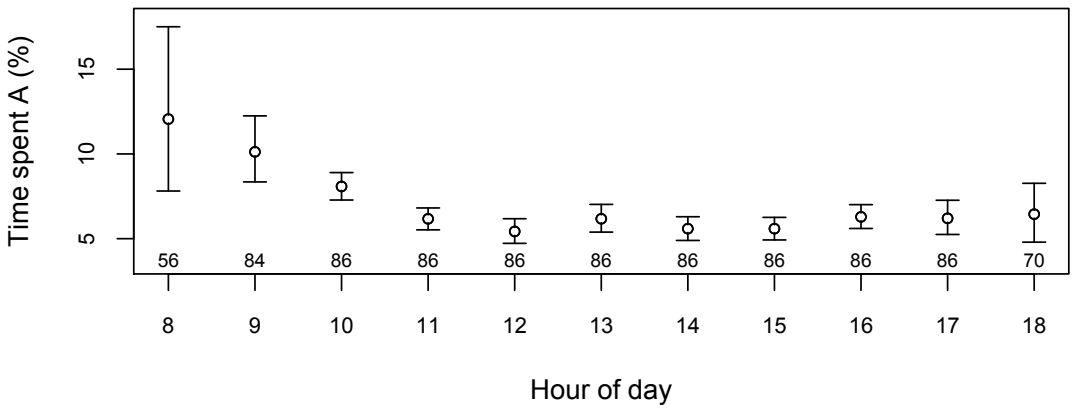
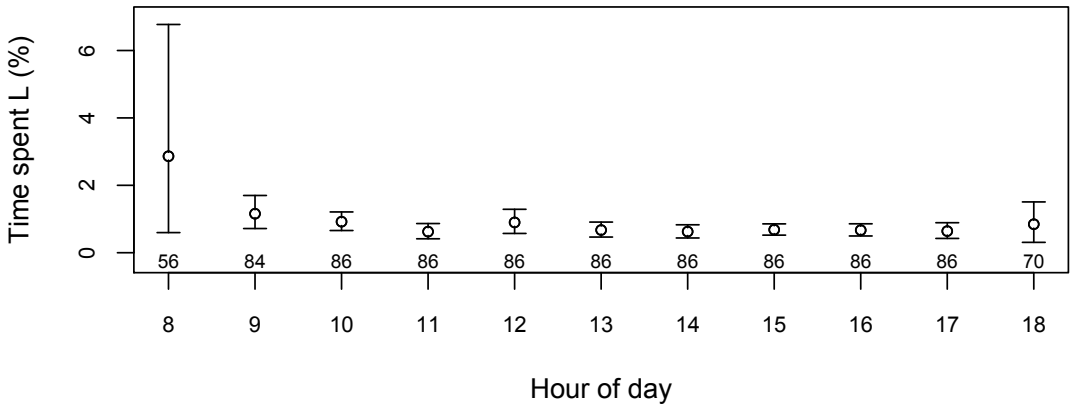
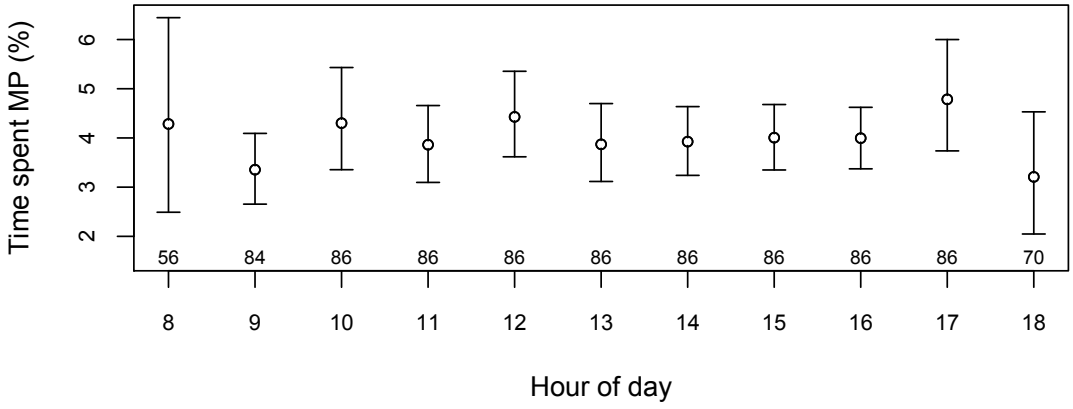
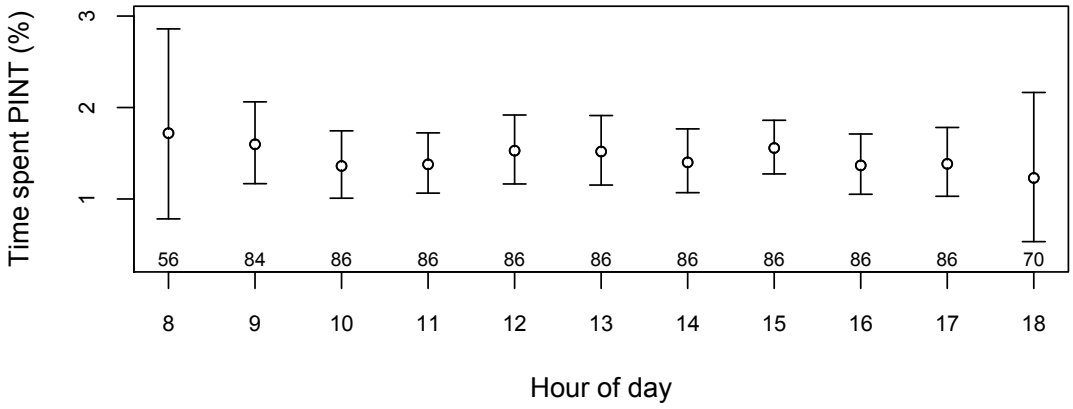
86
86
86
70
8
9
10
11
12
13
14
15
16
17
18
Hour of day

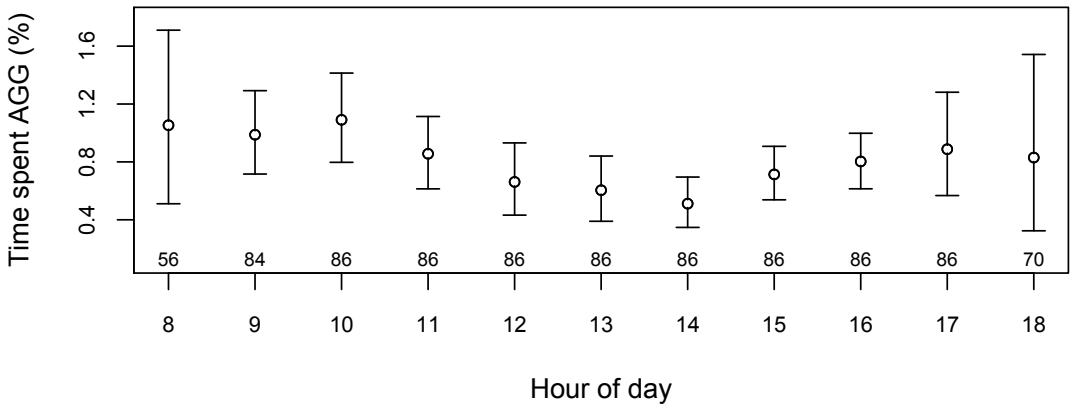

Time spent PC (%)
0
2
4
6
8
56
84
86
86
86
86
86
86
86
86
70
8
9
10
11
12
13
14
15
16
17
18
Hour of day


Time spent A (%)
5
10
15
56
84
86
86
86
86
86
86
86
86
70
8
9
10
11
12
13
14
15
16
17
18
Hour of day


Time spent L (%)
0
2
4
6
56 84 86 86 86 86 86 86 86 86 70
8 9 10 11 12 13 14 15 16 17 18
Hour of day


Time spent MP (%)
2
3
4
5
6
56 84 86 86 86 86 86 86 86 86 70
8 9 10 11 12 13 14 15 16 17 18
Hour of day


Time spent PINT (%)
1
2
3
56 84 86 86 86 86 86 86 86 86 70
8 9 10 11 12 13 14 15 16 17 18
Hour of day


Time spent AGG (%)
0.4
0.8
1.2
1.6
56 84 86 86 86 86 86 86 86 86 70
8 9 10 11 12 13 14 15 16 17 18
Hour of day

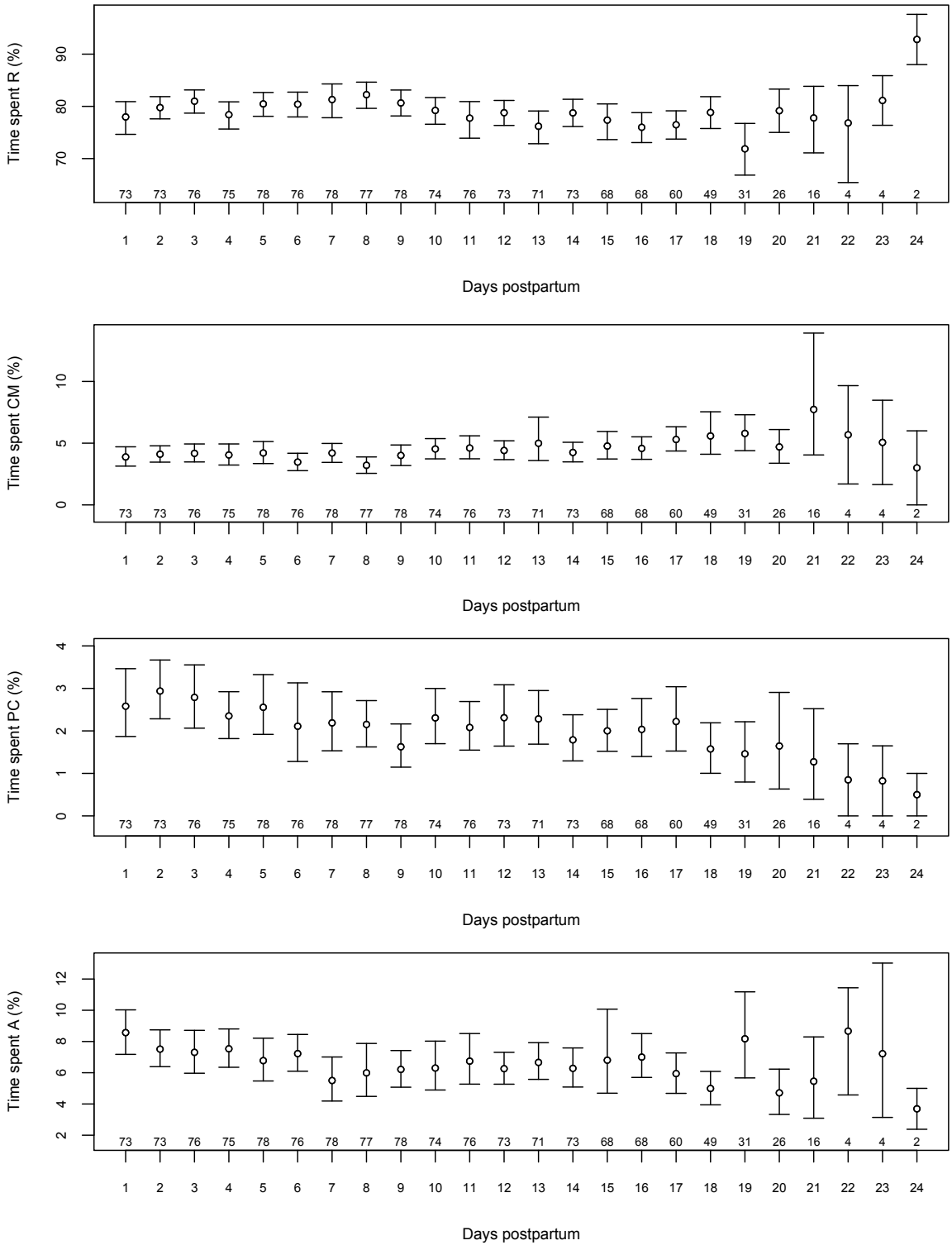
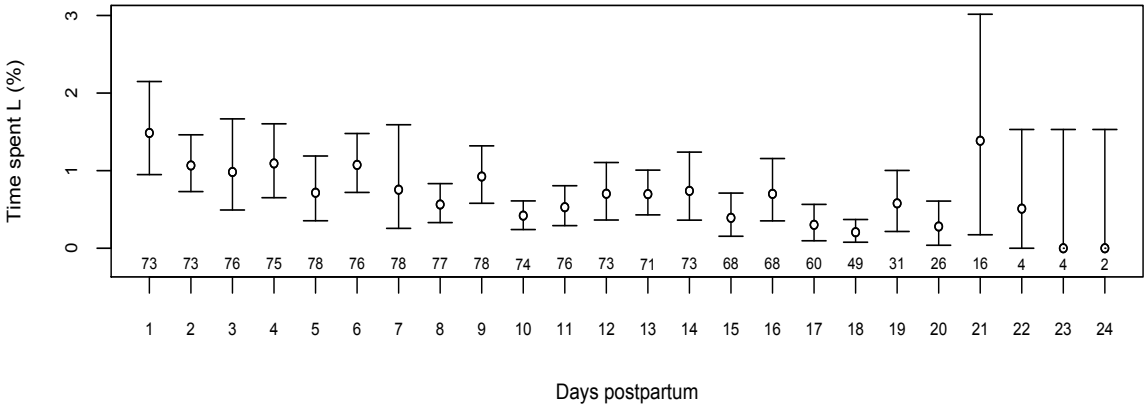
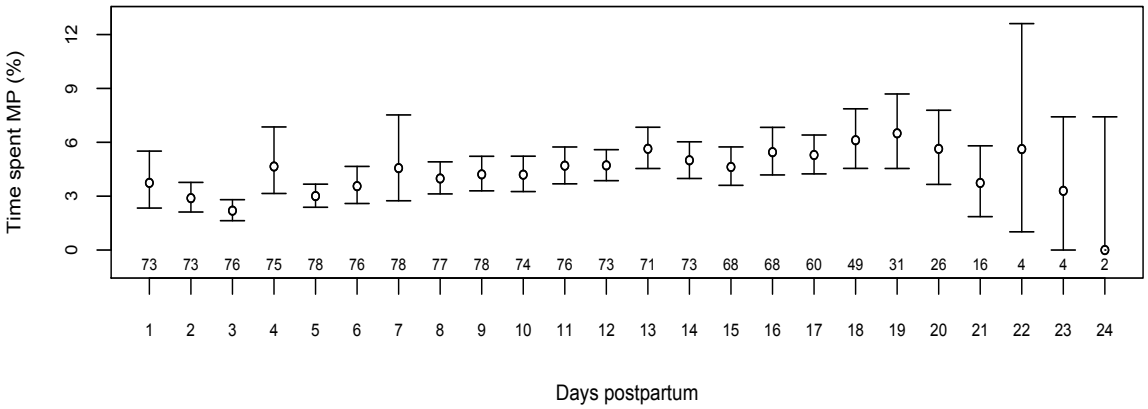
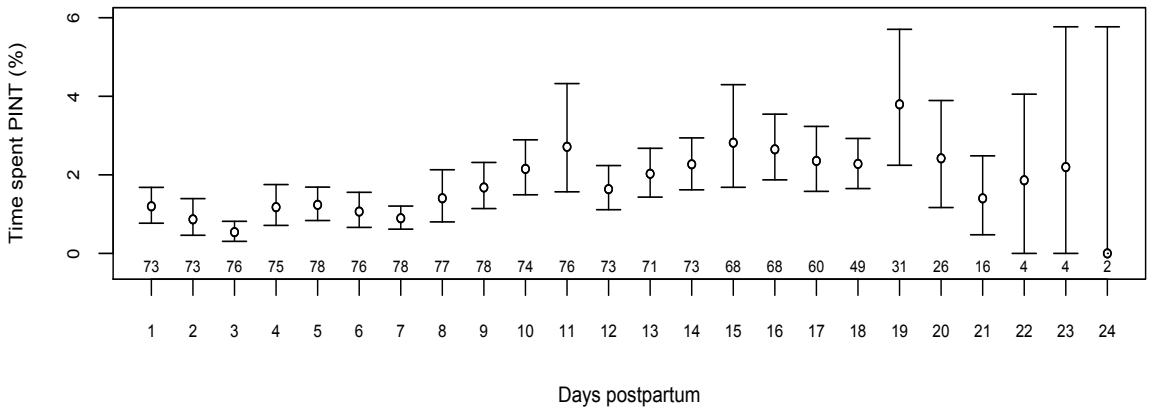
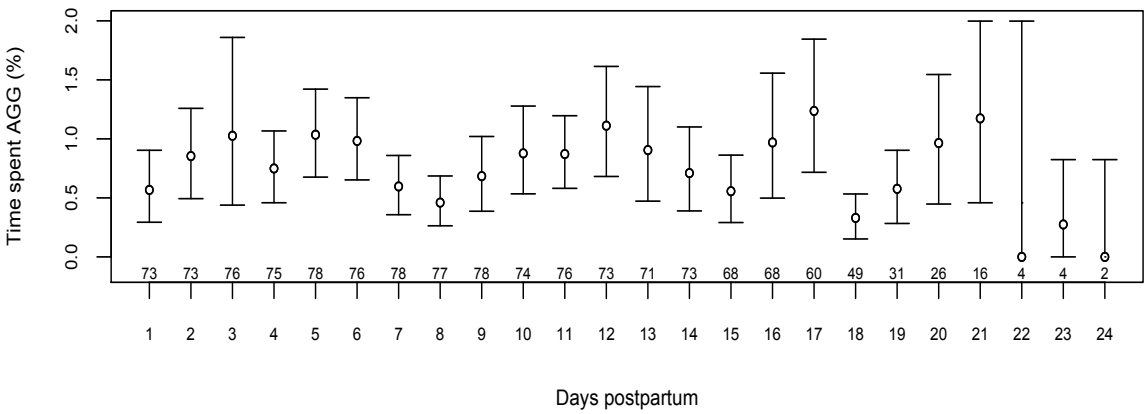


Figure 3.6: The pup age data for the percentage of time spent in each of the eight behavioural categories: resting (R), comfort movement (CM), pup check (PC) alert (A) locomotion (L) presenting & nursing (MP) pup interactions (PINT) aggression (AGG). On the x-axis, within the plot, the total number of individuals that make up the sample for each of the days postpartum is shown. The plots are continued over the page.


Time spent L (%)
0
1
2
3
73 73 76 75 78 76 78 77 78 74 76 73 71 73 68 68 60 49 31 26 16 4 4 2
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Days postpartum


Time spent MP (%)
0
3
6
9
12
73 73 76 75 78 76 78 77 78 74 76 73 71 73 68 68 60 49 31 26 16 4 4 2
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Days postpartum


Time spent PINT (%)
0
2
4
6
73 73 76 75 78 76 78 77 78 74 76 73 71 73 68 68 60 49 31 26 16 4 4 2
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Days postpartum


Time spent AGG (%)
0.0
0.5
1.0
1.5
2.0
73 73 76 75 78 76 78 77 78 74 76 73 71 73 68 68 60 49 31 26 16 4 4 2
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Days postpartum

3.8. Exploratory analyses of the covariates

The covariates were coarsely divided into three groups: 1) spatial data, 2) mother and pup data, 3) weather data. There were a number of complications with the weather data over the three years. These complications were outlined and addressed in Chapter 2 and as a consequence, the exploratory analyses of these data were also presented in the previous chapter (Chapter 2, Section 2.5.7). The exploratory analyses of the other two groups of covariates are detailed below.

3.8.1. The spatial covariates

There were seven spatial covariates extracted from the GIS database (Chapter 2, Section 2.5.6), these were:

1) Distance between the mother and her pup (m).
2) Distance between the mother and the nearest pool (m).
3) Distance between the mother and her nearest female neighbour (m).
4) Density of females around the mother using a 10 m buffer zone.
5) A measure of the mothers' home range usage (Kernel Density Estimate; Chapter 2, Section 2.5.6).
6) Inter-annual site fidelity (using 4 metrics, which are detailed below in Section 3.10).

The spatial covariates were considered to be a proxy for the local social and environmental variation that individuals experienced within and between breeding seasons. They were also considered to be a proxy for behaviour; in particular, site choice with reference to location of pools, and the mothers' positioning relative to her pup.

As noted in Section 3.4.1, four individuals were omitted from the gross dataset as a result of the exploratory analyses of the spatial data. In all four instances the individuals had few data points (ranging between 0 - 27) for at least one of the four spatial covariates. There was one other potential outlier, where the female maintained a comparably greater distance between her nearest female

neighbour (Figure 3.7). However, this individual had 115 data points, and after further investigation (checking field notes and assessing the behavioural data), there was no reason to omit her. The home range measure was not plotted, nor was it used to identify outliers because the KDE will range between 1 and 100, with a median closer to 100 (the core area of the estimated home range). Therefore, one would expect fewer data points closer to 1 and a greater number of data points closer to 100. Given that the site fidelity measures are applicable to re-sighted individuals only, these results shall be presented along with the exploratory analyses of the re-sighted individuals' datasets in Section 3.9.

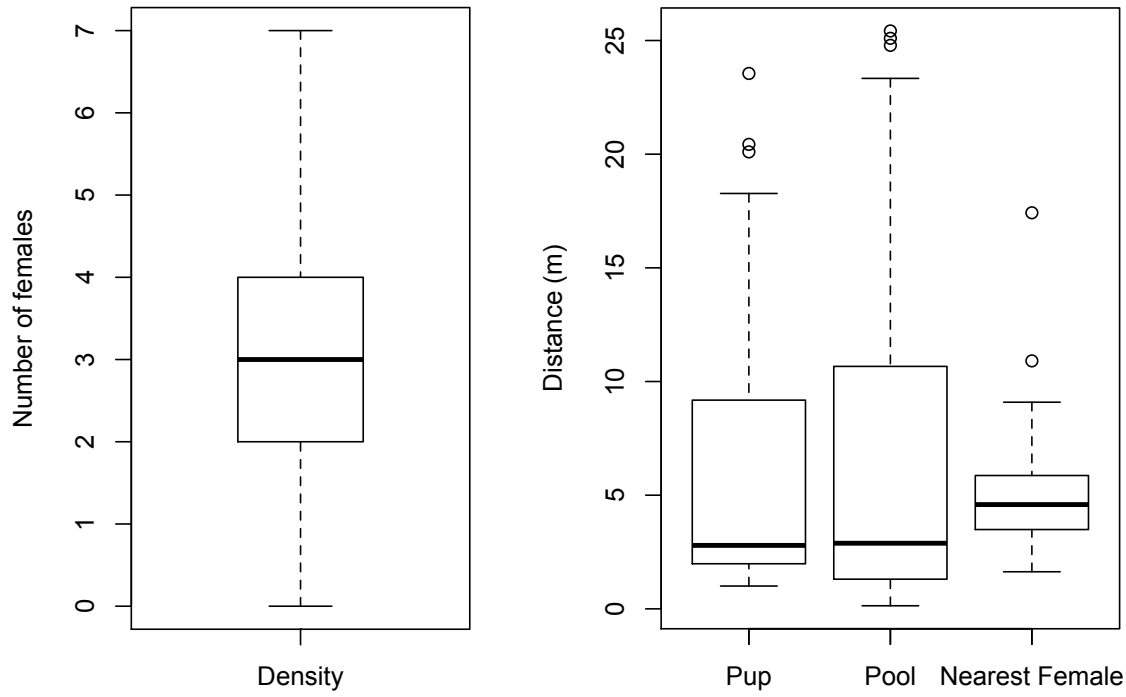


Figure 3.7: The gross spatial data for the postpartum females (n = 86) for: the density of females around the mother within a 10 m buffer zone (Density); the distance (m) between a mother and her pup (Pup); the distance (m) between a mother and her nearest pool (Pool); the distance (m) between a mother and her nearest female neighbour (Nearest Female). This plot uses the median value taken from each individual (n = 86) for each of the four covariates.

The median for the group of females was calculated using the median values for each individual (i.e. the median of the median). This was calculated as a weighted median (with the number of data points for each individual as the weights), using the weightedMedian() command in the *aroma.light* R package (Bengtsson et al., 2008). The gross spatial data showed that postpartum female grey seals tended to remain close to their pup (weighted median = 2.79 m) whilst maintaining a close distance to a pool of water (weighted median = 2.89 m). The weighted median distance to the nearest female neighbour was 4.59 m with 3 females typically within a 10 m radius of the mother (Figure 3.7).

3.8.2. Lactation period analyses of the spatial data

The lactation period analyses of the spatial data were carried out for the same reasons as detailed in Section 3.4 and using the same methodology. Of the five spatial covariates only the home range usage was significantly different between the lactation periods (Figure 3.8; Table 3.3). The *post hoc* multiple tests showed that there was higher variability in home range usage during the early lactation period. Whereas during the mid and late lactation periods the home range had a high median, and considerably less variability, with females spending more time closer to the core area of their estimated home range (Figure 3.8). This compliments the findings for the locomotion behavioural category, which decreased across the lactation periods, which suggests that females were moving more during the earlier stages of lactation.

3.8.3. Mother and pup covariates

The summary data for the mother and pup covariates only relate to females that were included in the gross dataset (n = 86). Therefore, these data are not necessarily representative of the NSA as a whole. In all three years there were a number of females that had already given birth before behavioural observations began (n = 3, 2007; n = 1, 2008; n = 4, 2009). Disregarding these, the date a female gave birth ranged from 30th September to 26th October. Similarly, in all three years there were a number of females that had not left the colony by the time the field team departed the island (n = 9, 2007; n = 4, 2008; n = 4, 2009; Tables

A3.1 - A3.3). Disregarding these individuals, the dates in which females left the colony ranged from 3rd October to 3rd November. Of these 86 females, 30 had male pups, 31 had female pups, and the sex of the other 25 pups was unknown. A total of 61 individuals were observed from giving birth to leaving the colony, with their duration of stay (postpartum) ranging between 12 to 25 days (median = 19; n = 61).

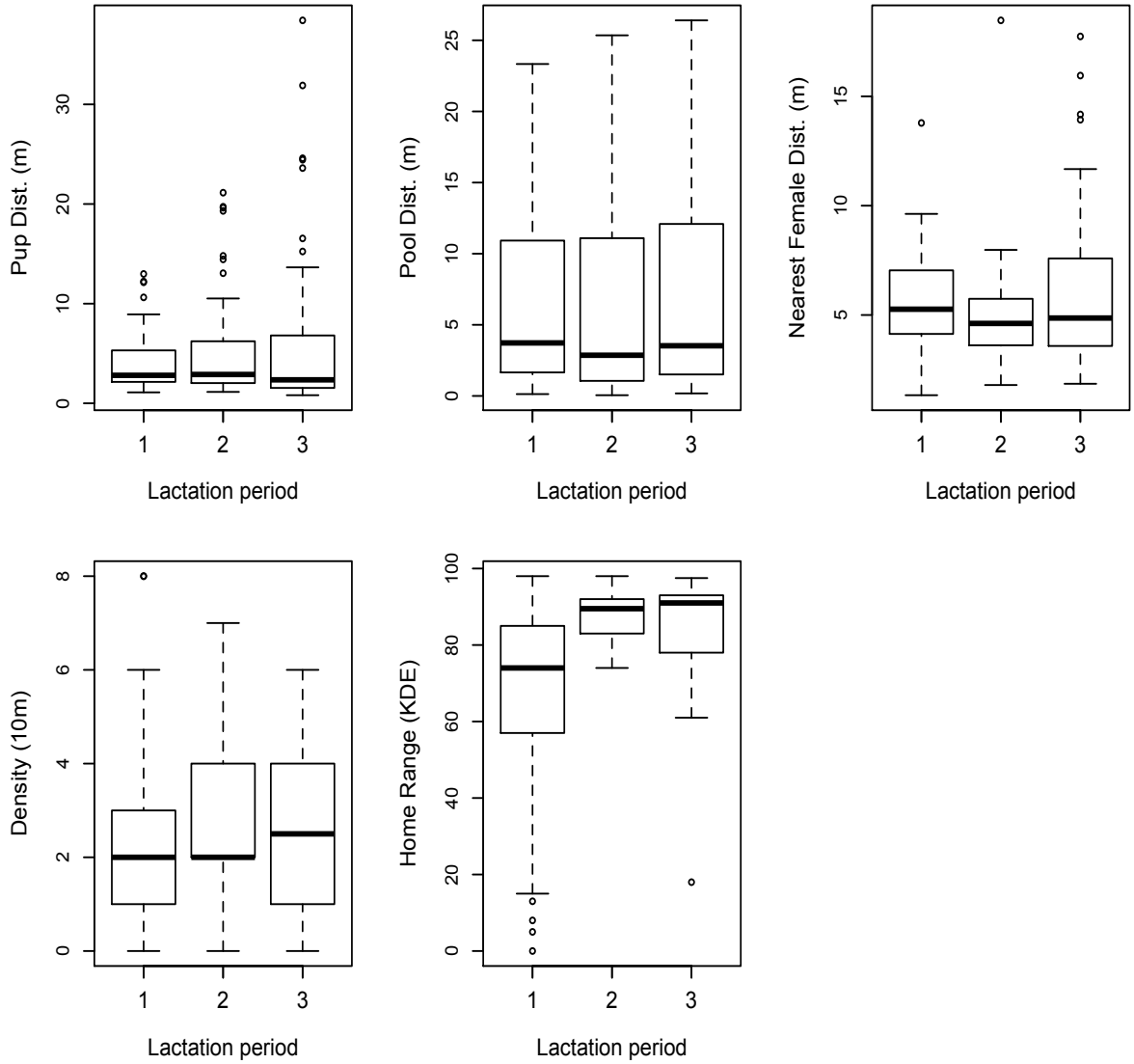


Figure 3.8: The lactation period analyses for the five spatial covariates: the distance (m) between a mother and her pup (Pup Dist.); the distance (m) between a mother and the nearest pool (Pool Dist.); the distance (m) between a mother and her nearest female neighbour (Nearest Female Dist.); the density of females within a 10 m buffer zone of the mother (Density); the location of the female within her estimated home range (Home Range, KDE), for the postpartum females (n = 61) for all three years (2007 - 2009) combined. The statistical analyses of these data are shown in Table 3.3.

Table 3.3: The results of the Kruskal-Wallis tests and the *post hoc* multiple comparison tests for the five spatial covariates during each of the three lactation periods (LP) for all females (n = 61) (LP1 n = 56; LP2 n = 59; LP3 n = 53) for all three years (2007 - 2009) combined. Significant results are in bold. The pairwise *post hoc* analyses show the observed and critical values (d.f. = 2). See Figure 3.8 for definitions of the metrics.

			LP1 - LP2		LP1 - LP3		LP2 - LP3	
Metric	Chi-Sq	*p*	Obs.	Crit.	Obs.	Crit.	Obs.	Crit.
Density	3.09	0.21	15.28	21.52	5.95	21.98	9.32	21.08
Pup	1.98	0.37	3.31	21.52	8.77	21.98	12.08	21.08
Pool	0.78	0.68	6.19	21.52	0.95	21.98	7.14	21.08
NFN	2.59	0.27	12.39	21.52	0.27	21.98	12.12	21.08
KDE	**28.48**	**<0.001**	**44.84**	**21.52**	**39**	**21.98**	5.83	21.08

3.9. Re-sighted individuals

There were 8 known individuals re-sighted in all three years; 10 additional known individuals were re-sighted in two consecutive years; and one known individual was re-sighted after skipping a year (not seen in 2008). However, two of the individuals re-sighted in two consecutive breeding seasons were omitted from the gross data set in one of the two breeding seasons in which they were re-sighted. Consequently, they were also removed from the re-sighted individuals' datasets. In both instances these individuals were omitted due to a lack of spatial data. Given that the spatial data are critical to the analyses presented in the following three chapters, and given that the re-sighted individuals' datasets are compared throughout the thesis, it was deemed important to maintain consistency with respect to which individuals were included at each step of the analyses. Consequently, after omitting these two individuals, there were a total of 17 re-sighted individuals (N = 17) that were included in the subsequent analyses. All of the exploratory analyses presented hereafter shall only use the re-sighted individuals' datasets.

3.10. Site fidelity analyses

There were four measures of site fidelity calculated between successive breeding seasons. These were; the distance between pupping sites (m); the distance between the centre of the core area of an individuals' home range (m); and the percentage overlap between the 50% and 90% KDE isopleths (Chapter 2, Section 2.5.6). The site fidelity measures were calculated for consecutive years (2007 & 2008 and 2008 & 2009) and for non-consecutive years (2007 & 2009). The data for the first two measures are shown in Table 3.4 and the data for the latter two measures are shown in Table 3.5.

The site fidelity of re-sighted females varied considerably (Table 3.5) for both the distance between pupping sites, which ranged from 3.82 m to 66.52 m (median = 16.55 m) and for the distance between the centre of the core area of the home range, which ranged from 1.3 m to 48.15 m (median = 17.5 m). The distance between pupping sites presented here is lower than reported by previous studies on North Rona (median = 55 m, Pomeroy et al., 1994; median = 39 m, Pomeroy et al., 2005). However, this is likely to be an artefact of the NSA, which is considerably smaller than the Study Area (SA), where the previous pupping site fidelity measures were taken from. This individual variation in site fidelity was also shown in the overlap between the KDE isopleths between breeding seasons (Table 3.5). For example, some individuals were consistently returning to the same area (e.g. 903 and 908), whereas other individuals' home range usage did not overlap at the 50% or at the 90% KDE isopleths (e.g. 906 and 914). For a visual comparison of the individual variation in home range usage between breeding seasons, the 5%, 50% and 90% KDE isopleths for a selection of the re-sighted individuals are plotted in Figure 3.9.

Both of these metrics were included as they are likely to have different biological implications with reference to habitat selection and habitat use. For example, both the pupping site and the centre of the core area of the home range may be influenced by social (Pomeroy et al., 2005) and environmental (e.g. availability of pools; Redman et al., 2001) conditions. However, the latter may be

influenced by changes in environmental conditions that occur during lactation, which may also include the behaviour of the mothers' pup and/or conspecifics.

Table 3.4: The site fidelity measures for the distance (m) between a female's pupping sites (Pup) and the centre of the core area of their estimated home range (Cent.) between pairwise breeding seasons; the age of the pup when the pupping site location was recorded was one day old in most cases (see footnote). A grey cell indicates that the individual was not seen in one of the two breeding seasons.

	2007 & 2008		2008 & 2009		2007 & 2009	
ID	Pup	Cent.	Pup	Cent.	Pup	Cent.
901[a]	19.86	15.31	9.52	20.1	25.9	22.06
902	9.61	9.1	13.42	42.63	3.82	35.49
903	21.36	6.93	12.85	5.66	33.9	2.75
904	18.64	20.84	21.32	31.49	36.13	47.9
905	16.24	29.38	25.48	23.38	9.88	6.44
906	46.44	44.84	47.71	42.25	66.52	28.64
907[a]	24.77	17.41	53.03	48.15	40.9	41.42
908	16.24	3.22	13.94	1.3	12.53	4.39
909					42.42	15.81
910			13.64	11.04		
911			13.92	17.5		
912[b]			13.26	11.6		
914[c]			43.21	43.97		
915			16.55	18.24		
916			9.86	17.24		
917			10.52	12.78		
919	5.81	15.63				

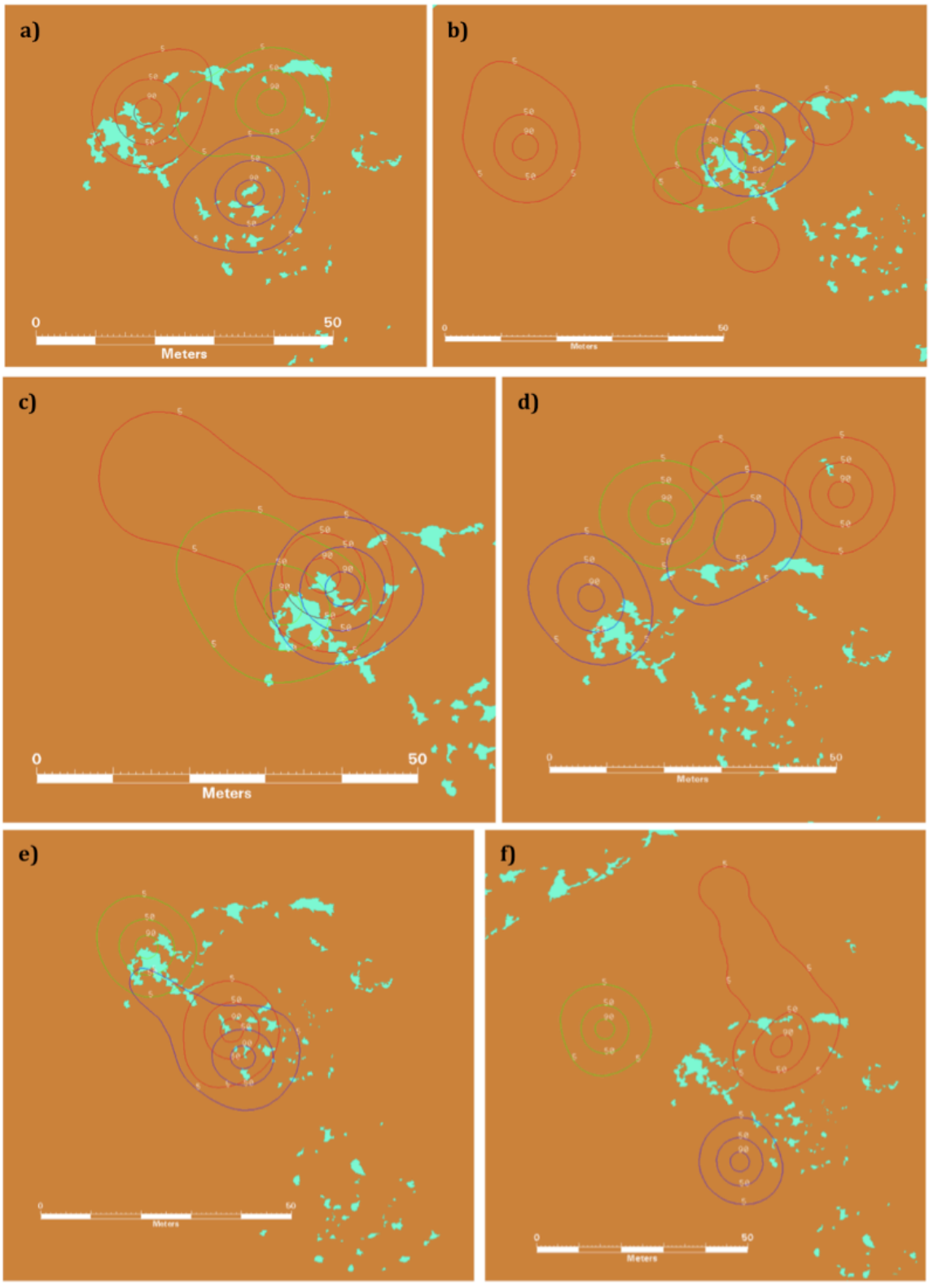
[a,b,c]: In 2009 the pups of these females were not mapped until they were 3[a], 5[c] and 9[b] days old

Table 3.5: The percentage (%) overlap of the 50% and 90% Kernel Density Estimates between pairwise breeding seasons for each of the re-sighted females. A grey cell indicates that the individual was not seen in one of the two breeding seasons.

	2007 & 2008		2008 & 2009		2007 & 2009	
ID	50%	90%	50%	90%	50%	90%
901	0	15.23	0	9.37	0	0
902	24.8	39.06	0	0	0	0
903	24.44	33.75	29.39	34.63	40.97	30.87
904	0	15.67	0	0	0	3.77
905	0	0	0	0	33.23	41.48
906	0	0	0	0	0	0
907	0	19.5	0	0	0	0
908	42.68	45.92	44.5	43.97	39.32	44.03
909					0	15.66
910			6.57	33.64		
911			0	16.37		
912			5.69	28.89		
914			0	0		
915			0	25.06		
916			26.09	44.97		
917			0	28.1		
919	0	32.05				

The following two pages show:

Figure 3.9: The 5%, 50% and 90% isopleths for the re-sighted individuals: **a)** 901, **b)** 902, **c)** 903, **d)** 904, **e)** 905, **f)** 906, **g)** 907, **h)** 908, **i)** 910, **j)** 914, **k)** 916, **l)** 919. The blue, green and red isopleths show the home range usage of the re-sighted individuals in the 2007, 2008 and 2009 breeding seasons, respectively. Pools of water are shaded blue and were digitised using the aerial photograph from the survey on 17th October 2008 (Chapter 2, Section 2.5.5). All of the scale bars are to 50 m. The isopleths are labelled.


a)
0
50
Meters
b)
c)
0
50
Meters
d)
e)
f)

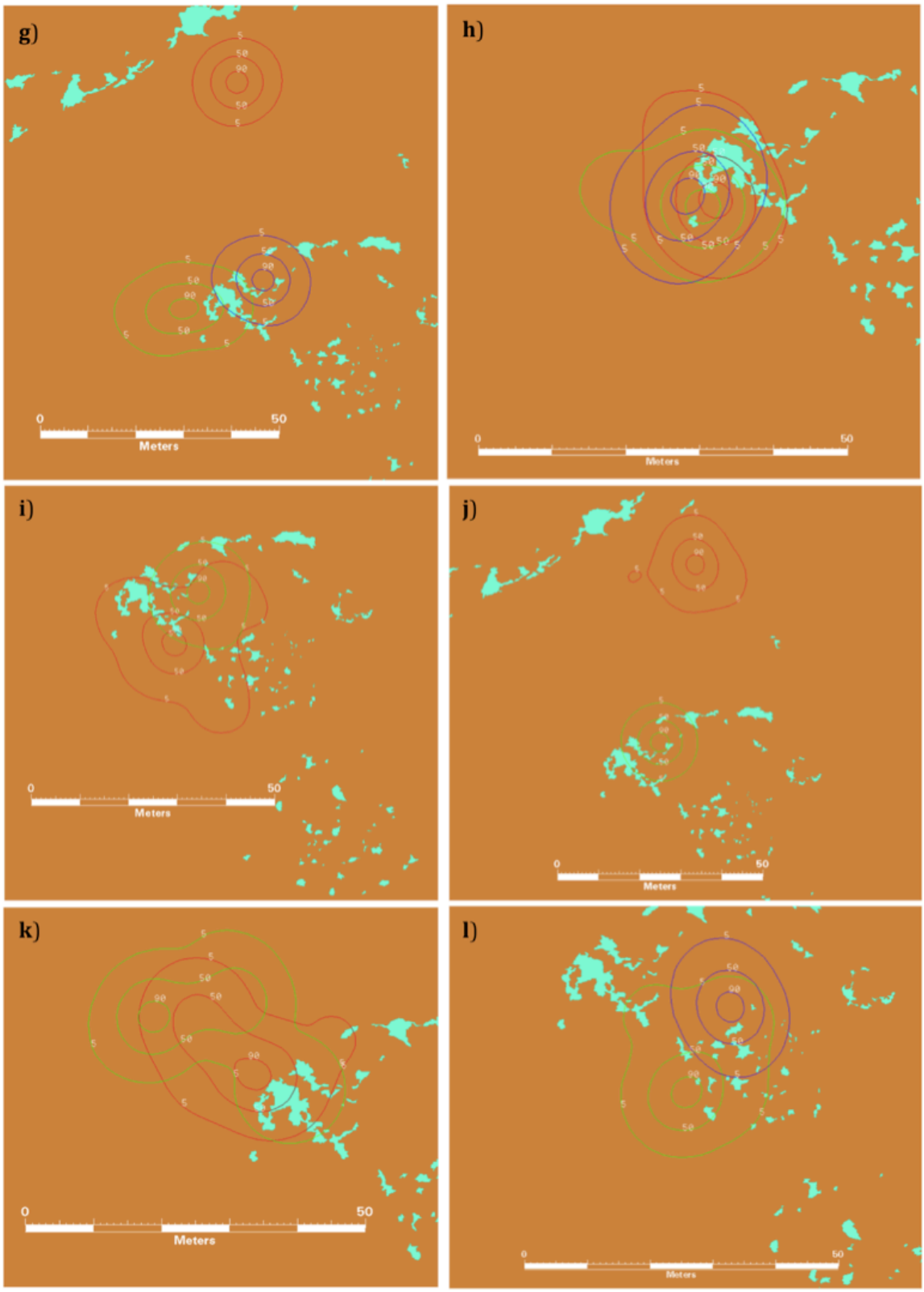

g)
h)
i)
j)
k)
l)
0
50
Meters

Table 3.6: The distance (m) between the pupping site and the centre of the core area of the home range within each of the breeding seasons for the re-sighted individuals. The age of the pup when the pupping site location was recorded was one day old in most cases (otherwise pups were 3[a], 5[c] and 9[b] days old). A grey cell indicates that the individual was not seen during the given breeding season.

ID	2007	2008	2009
901	4.31	9.38	1.88 [a]
902	1.59	3.52	32.63
903	5.51	11.71	25.79
904	1.9	3.71	14.58
905	15.07	3.58	6.85
906	1.11	3.23	40.71
907	1.32	7.22	1.29 [a]
908	2.82	16.92	14.76
909	13.41		25.12
910		2.57	16.15
911		4.33	8.55
912		4.7	4.52 [b]
914		0.88	12.22 [c]
915		7.21	11.84
916		13.29	11.77
917		2.31	5.85
919	2.31	12.63	

Previous research has shown that during lactation, females typically move less than 10 m from their pupping site (Aust & Pomeroy, unpublished data) and rarely move further than 10 m from their pup (Redman et al. 2001). The distance between the pupping site and the centre of the core area of the home range within a breeding season support the former finding (median = 5.85 m; Table 3.6), whilst the gross spatial data for the distance between a mother and her pup support the latter finding (weighted median = 2.79 m; Figure 3.7). Furthermore, the lactation

period analyses of the spatial data presented in Section 3.8.2 did show a shift in home range usage after the first few days postpartum which suggests that the transition between spending time at the pupping site and spending time at the centre of the core area of the home range occurred shortly after the first few days postpartum. Therefore, on an albeit fine spatial scale, the location of an individual's pupping site and the location of the centre of the core area of their home range are likely to be in geographically different locations.

3.11. Hourly activity budget

Given that the gross activity budget is a rather coarse overview of female grey seals' behaviour whilst on the breeding colony, the data were also divided into hourly activity budgets for every day that data were collected. In Chapters 5 and 6 these data are modelled at this temporal scale, which was selected because all of the potential explanatory variables were recorded at an hourly interval with the exceptions of rainfall, which was recorded once every day, and pup behaviour, which was recorded every 5 minutes (Chapter 2, Section 2.5.4). Given that pup behaviour was recorded at the same temporal scale as the mothers' behaviour, it would have been possible to model the data at 5 minute intervals. However, in order to model these data in such a manner, the sequence in which the mother and pup were sampled would have had to be maintained throughout the study in order to control for who was responding to whom. Furthermore, to select which individual was sampled first would require a hypothesis based on whether the mother responds to the pup or the pup responds to the mother, which is not likely to be a straightforward relationship (e.g. Kovacs, 1987; Smiseth & Lorentsen, 2001). In addition, given the very short duration between sampling the mother and her pup (or vice versa; ca. < 5 seconds), it is unlikely that individuals would always be in a position to respond to behaviour over such a short interval (e.g., if the mother and her pup were not geographically close to one another). Consequently, the proportion of time a pup spent active within an hour was used as an explanatory variable (see below).

Converting the activity budget to an hourly temporal scale means that, for an individual, the maximum number of scan samples per hour is 12. The

distribution of the total number of scan samples collected per hour is displayed in Table 3.7. These data show that the total number of occurrences where an individual had a full compliment of 12 scan samples in an hour was approximately 60% (Table 3.7). There are two reasons why individuals would have less than 12 scan samples per hour: (1) a lack of daylight meant that it was not possible to gather data over the entire first and last hour of the day and (2) if the individual was out-of-sight during a scan sample. Furthermore, the 2007 sampling protocol, where scan samples were interspersed with focal samples (Chapter 2, Section 2.5.4), would greatly reduce the occurrence of individuals with a total number of 12 scan samples per hour. The 2007 sampling protocol is also likely to explain the second peak in these data, where the total number of scan samples per hour was 6.

Table 3.7: The distribution of the total number of scan samples collected per hour for females and pups (n = 4732), the numbers in parenthesis show the total percentage (%).

Number of scan samples per hour	Total Number of occurrences: mother	Total Number of occurrences: pup
12	2773 (58.6)	1597 (33.75)
11	124 (2.62)	342 (7.23)
10	128 (2.7)	353 (7.46)
9	116 (2.45)	262 (5.54)
8	106 (2.24)	222 (4.69)
7	179 (3.78)	230 (4.86)
6	379 (8.01)	385 (8.14)
5	247 (5.22)	281 (5.94)
4	167 (3.53)	229 (4.84)
3	133 (2.81)	229 (4.84)
2	156 (3.3)	263 (5.56)
1	224 (4.73)	339 (7.16)

The fine-scale datasets shall be analysed using a weighted linear regression (see Chapters 5 and 6). Therefore, the total number of scan samples per hour shall be considered (i.e. weighted) in these analyses. However, given that the activity of the pup was calculated as a proportion per hour it is possible that a relationship between the number of scan samples collected and the proportion of time spent active could occur. The distribution of the total number of scan samples per hour for the pups had a greater spread, with approximately 35% of the behavioural data collected from individuals with 12 scan samples per hour (Table 3.7). As it is not possible to weight a covariate in the linear regressions presented in Chapters 5 and 6, it is important to assess whether or not there are any biases in these data relating to the proportion of time spent active and the number of samples collected, in order to avoid spurious conclusions.

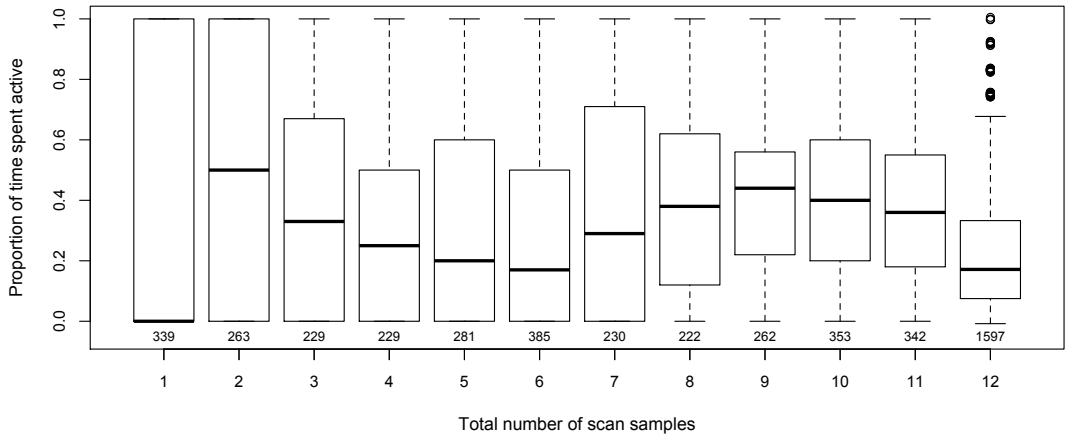


Figure 3.10: The proportion of time that pups (n = 40) of re-sighted females spent active is plotted against the total number of scan samples collected per hour for all three years (2007 - 2009) combined. The sample size for each of the total number of scan samples is shown on the x-axis, inside the plot.

The pup activity was calculated as the proportion of time the pup spent performing behaviours defined within the active behavioural category per hour (Chapter 2, Section 2.5.3). Figure 3.10 shows the proportion of time the pup spent active plotted against the total number of scan samples recorded per hour. There was a significant difference between the proportion of time spent active for groups

of data, based on the total number of scan samples collected per hour (ANOVA, $F_{(1,4730)} = 178.23$; $p < 0.001$); however, there is no clear pattern that suggests that the proportion of time spent active decreases with sample size, for example. To be thoroughly confident that there was no pattern in these data the same plot was reproduced for each of the re-sighted females' pups for each of the three years. A subset of these plots is shown in the Appendix (Figures A3.1 - A3.3). Similarly, none of these plots showed any pattern that suggested that there was a relationship between the number of scan samples per hour and the proportion of time the pup spent active.

3.12. Checking for independence

Independence of data is assumed for the majority of statistical analyses. In order to avoid violating this assumption, information from any one observation should not provide information on another (Hurlbert, 1984). If a lack of independence is ignored then the likelihood of a type I error is increased (incorrectly rejecting the null hypothesis; Hurlbert, 1984; Heffner et al., 1996; Zuur et al., 2009a). A formal way to test for temporal dependence is to plot autocorrelation functions (ACFs) for regularly spaced time series. The ACF calculates the Pearson correlation between a time series and the same time series shifted by *k* time units (Zuur et al., 2009a, b).

In the current study, it is possible that temporal autocorrelation may occur in the hourly activity budgets. In order to assess this, the ACF was used to plot all of the re-sighted individuals collectively for each breeding season for each of the eight behavioural categories. These plots were used to assess whether or not temporal autocorrelation in behaviour occurred across the study population as a whole. More relevant to the subsequent analyses, the ACF was also used to plot each of the re-sighted females individually, for each of the breeding seasons and for each of the eight behavioural categories. These plots were used to assess whether or not temporal autocorrelation in behaviour occurred at the individual-level. A subset of the ACF plots is shown in the Appendix (Figure A3.4). Not all plots were presented because the total number of ACF plots approached 850. Every ACF plot was assessed and there was no evidence that temporal

autocorrelation in behaviour occurred at the population-level or the individual-level. Therefore, analysis of the response variables at this temporal scale does not violate the assumption of independence.

3.13. Checking for zero inflation

Zero inflation occurs when a dataset has such a large number of zeros that it does not fit a standard distribution (e.g. Binomial or Poisson; Martin et al., 2005; Zuur et al., 2009a, b). The occurrence of a large number of zeros is a common feature of ecological datasets, and arguably more so for behavioural data. This can be caused by 'true zeros', which are a result of real ecological effects such as rare events, or by 'false zeros', which are a result of sampling or observer error (e.g., in a presence/absence study if the observer fails to record an individual that is present).

In the present study, as a result of the resting behavioural category accounting for ca. 80% of an individual's activity budget (Table 3.1), it is likely that there will be a considerable number of 'true zeros' recorded in the other seven behavioural categories. To visually assess whether or not any of the behavioural categories may be zero inflated, the frequency in which the number of times a behaviour was observed, per hour was plotted (Figure 3.11). As expected, all of the behavioural categories, with the exception of resting, have a considerably high number of zeros. Nevertheless, this does not necessarily mean that these behavioural categories are zero inflated (Martin et al., 2005; Bolker, 2008; Zuur et al., 2009a, b). An analytical assessment of zero inflation shall be carried out in Chapters 5 and 6, prior to modelling the data.

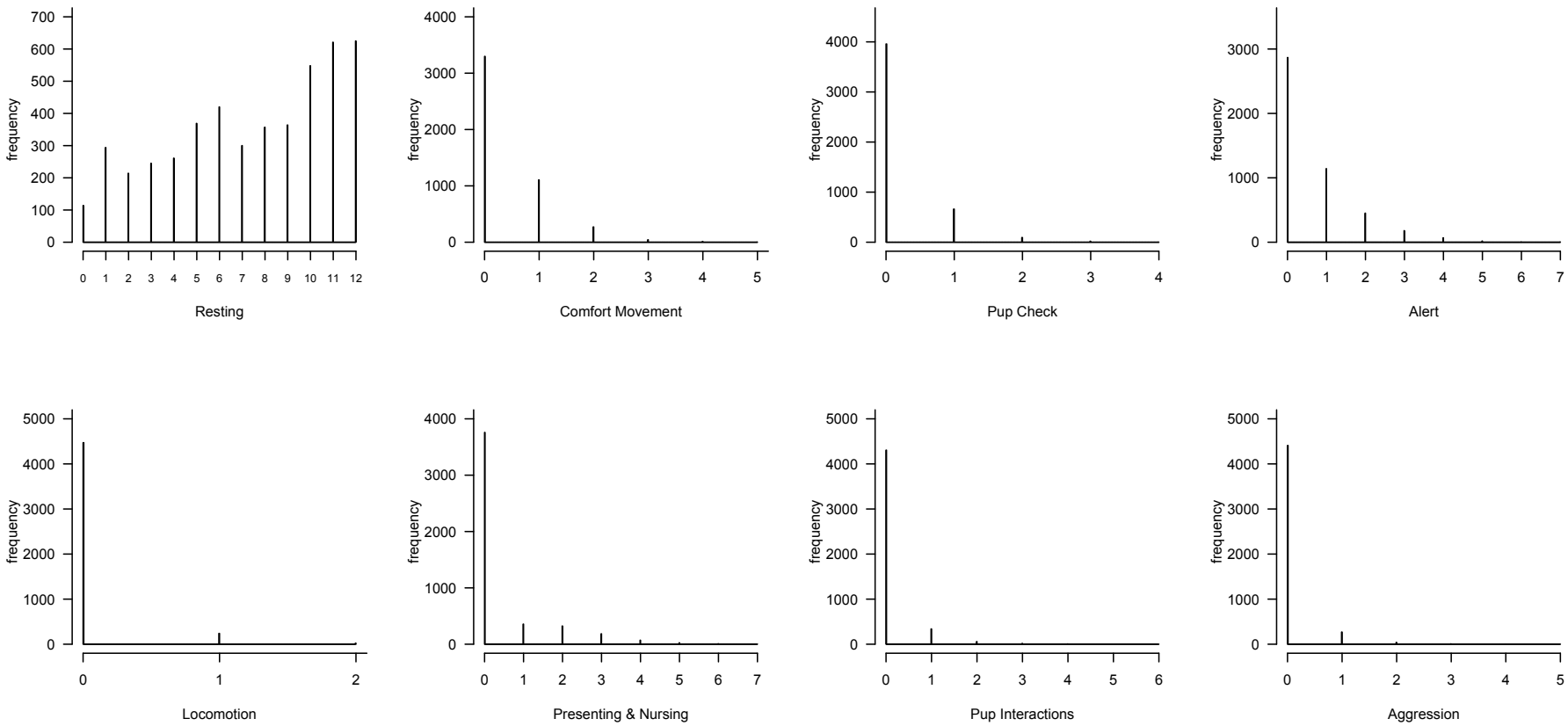


Figure 3.11: The number of times each of the behavioural categories was recorded per hour for all re-sighted postpartum females (N = 17) over the three breeding seasons (2007 - 2009); the behavioural category is shown on the x-axis. The number of times the behaviour was observed per hour is shown on the x-axis. There are observations for each of the maximum occurrences displayed on each of the x-axes; however, given that several behavioural categories have a considerably higher frequency at lower occurrences, the lower frequencies at higher occurrences may be indistinguishable in some instances.

3.14. Collinearity between covariates

The collinearity of the covariates is addressed here but is not analytically relevant until Chapters 5 and 6. Nevertheless, it was decided to present these data here in order to minimise the need for exploratory analyses in the subsequent chapters, where the principal aim is to model these data. In the aforementioned chapters, the data are analysed such that the groups of individuals that are re-sighted in pairwise years (2007 & 2008, 2008 & 2009, 2007 & 2009) and in all three years (2007 - 2009) are analysed annually. Therefore there are a total of 9 re-sighted individuals' datasets. Although these are the same groups of individuals, based on personal observations and the results of the exploratory analyses presented in this chapter, there were important environmental differences between the breeding seasons that may not be evident in the model output if both (or all three) years' data are included in one analysis. Therefore, modelling each of the years separately is expected to compliment the fine-scale nature of the study, albeit at the cost of reducing the size of the dataset used in the analysis. In addition, by using this method the data do not violate independence (i.e. there is no pseudoreplication of individuals across years). Correcting for multiple comparisons was not undertaken (e.g. Bonferroni correction) because there is evidence that such corrections are unnecessary and may even be deleterious to sound statistical inference (Perneger, 1998). However, if one were inclined to use a more conservative level of significance, for example, $p < 0.01$, then the majority of the significant correlations discussed below (which consider $p < 0.05$ as significant) would still be considered significant.

The continuous covariates that were used in the analyses were; 1) the proportion of time the females' pup was active, 2) the density of females within a 10 m buffer zone of the target female, 3) the distance between a female and her nearest female neighbour (m), 4) the distance between a female and her pup (m), 5) the distance between a female and her nearest pool (m), 6) the location of a female within her estimated home range (KDE), 7) rainfall (mm), 8) air temperature (^{o}C), 9) the age of the pup (days postpartum). See Chapter 2, Section 2.5 and, in the current chapter, Section 3.8, for more details on how these data were collected and derived.

Despite the diurnal patterns that were evident in some of the behavioural categories (Section 3.7.2), the hour of the day was not included in the analyses. This is because the diurnal (and seasonal; Section 3.7.1) variation in behaviour is likely to be the product of extrinsic (external) factors that are explained by other covariates, such as density, rainfall and air temperature (which are included in the subsequent analyses). Conversely, the age of the pup (Section 3.7.3) was included in the analyses because it may identify behavioural variation during lactation that was not influenced, or entirely influenced, by extrinsic factors. Specifically, behavioural variation over the course of lactation may, to some degree, be influenced by intrinsic factors (such as the condition of the mother). Given that the lactation periods (Sections 3.6 and 3.8.2) are a coarse measure of the number of days postpartum, they were omitted from the subsequent analyses.

As expected, many of the covariates were found to be collinear with one another (Tables A3.4 - A3.12) and several covariates maintained their collinearity irrespective of which re-sighted individuals' datasets were used (Tables A3.4 - A3.12; Figure 3.12). The major findings of the collinearity analyses are summarised below, and the methods used for dealing with collinearity in the analyses presented in the following chapters are discussed.

The distance between a mother and her pup and the distance between a mother and the nearest pool had a strongly significant, negative relationship in all 9 analyses (min. r = -0.17, max. r = -0.47, $p < 0.001$, n = 9; Tables A3.4 - A3.12). Therefore, the closer the mother was to the pool, the further away she was from her pup. This finding is not unexpected, given that previous studies have shown that there is an important relationship between maternal attendance and the availability of water (Twiss et al., 2000; Redman et al., 2001).

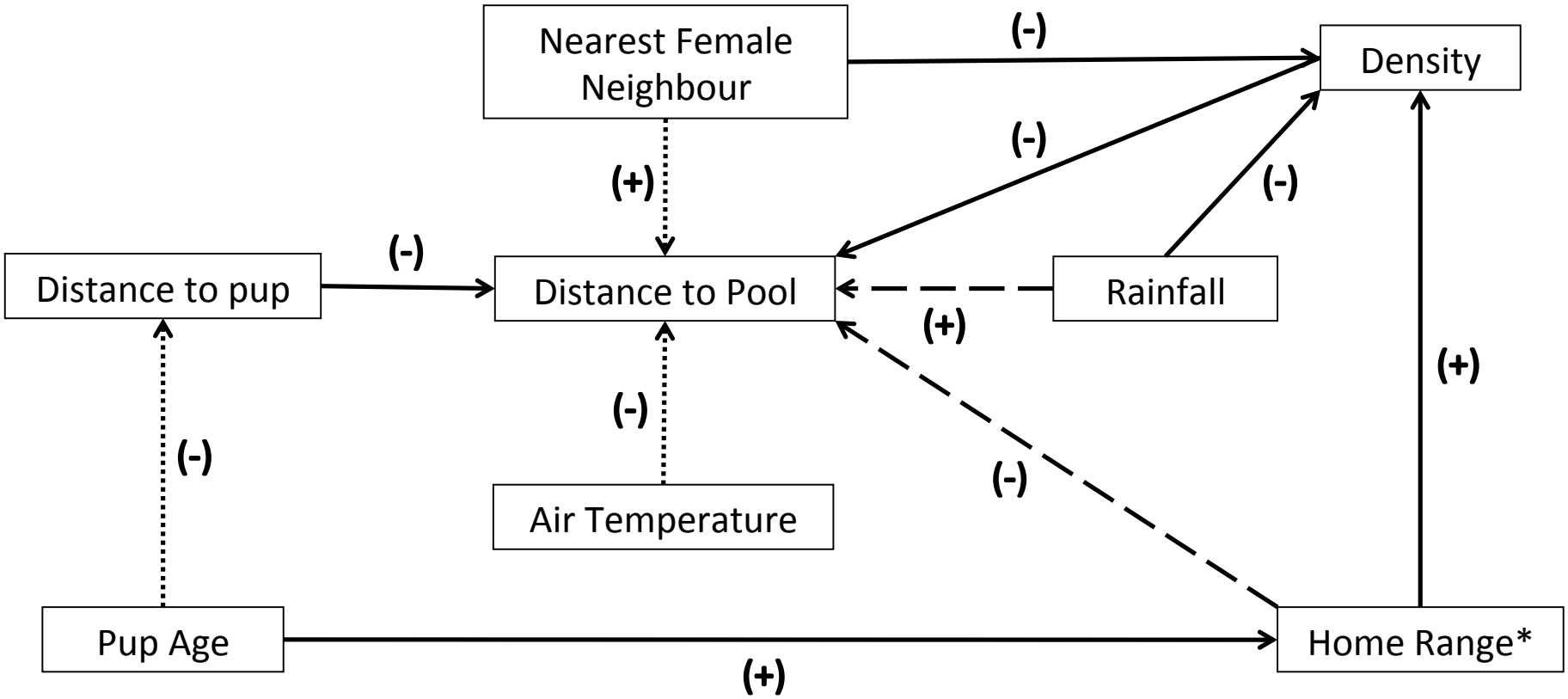


Figure 3.12: The covariates that were collinear in the majority of the re-sighted individuals' datasets (Tables A3.4 - A3.12). The direction of the correlation is shown in parenthesis adjacent to the arrow. For example, as the rainfall increases the density decreases; as rainfall increases the distance to the nearest pool increases. The solid arrows indicate those that were collinear in all three breeding seasons; the dashed arrows indicate those that were collinear in the 2008 and 2009 breeding seasons; the dotted arrows indicate those that were collinear in the 2007 and 2008 breeding seasons. *For the home range metric, the higher the value, the closer the female is to the centre of the core area of her estimated home range.

The density measure was found to be collinear with the nearest female neighbour, the distance to the nearest pool, the home range metric, and the amount of rainfall. With the exception of home range, all of these relationships were negative (Tables A3.4 - A3.12). Once again, these relationships were not surprising. In particular, the fact that the higher the density of females around the mother, the closer the nearest female neighbour is, is to be expected. In addition, given that pools of water are known to be important to postpartum females whilst on the breeding colony (Twiss et al., 2000; Redman et al., 2001), it is unsurprising that density was greater the closer the mother was to the pool. Furthermore, this does tie in with the estimated use of an individual's home range such that the density increases the closer the mother is to the core area of her home range. Yet, the distance to the nearest pool and the home range metric was not significantly collinear across all 9 of the re-sighted individuals' datasets.

On closer inspection of the data, it is only the three analyses from 2007 that show no evidence of collinearity between the distance to the nearest pool and the home range metric (Tables A3.4, A3.7 and A3.11). Interestingly, this year was considerably drier from the beginning to the middle of the breeding season, as compared with 2008 and 2009 (Figure 3.13). Also, at the beginning of the 2007 breeding season, it was comparatively warmer (Figure 3.14). Consequently, with fewer pools to congregate around in 2007, the relationship (collinearity) between the distance to the nearest pool and the home range metric could have been disrupted. This supposition is supported by a previous study, which showed that during drier periods females did have to commute longer distances to gain access to pools of water (Redman, et al., 2001). Therefore, females preferred to have the centre of the core area of their home range close to a pool; however, extreme environmental stress as a result of considerably less rainfall, and perhaps to a lesser extent, warmer conditions, caused this relationship to break down.

A particularly interesting result from all 9 of these analyses was that when rainfall increased, density decreased (min. $r = -0.075$, max. $r = -0.6$ min, $p < 0.001$, max. $p = 0.012$, $n = 9$). Similar to the relationship with the distance to the pool and the home range metric, the distance to the nearest pool and the amount of rainfall had a strongly significant positive relationship in 2008 and 2009 (min. $r = 0.09$,

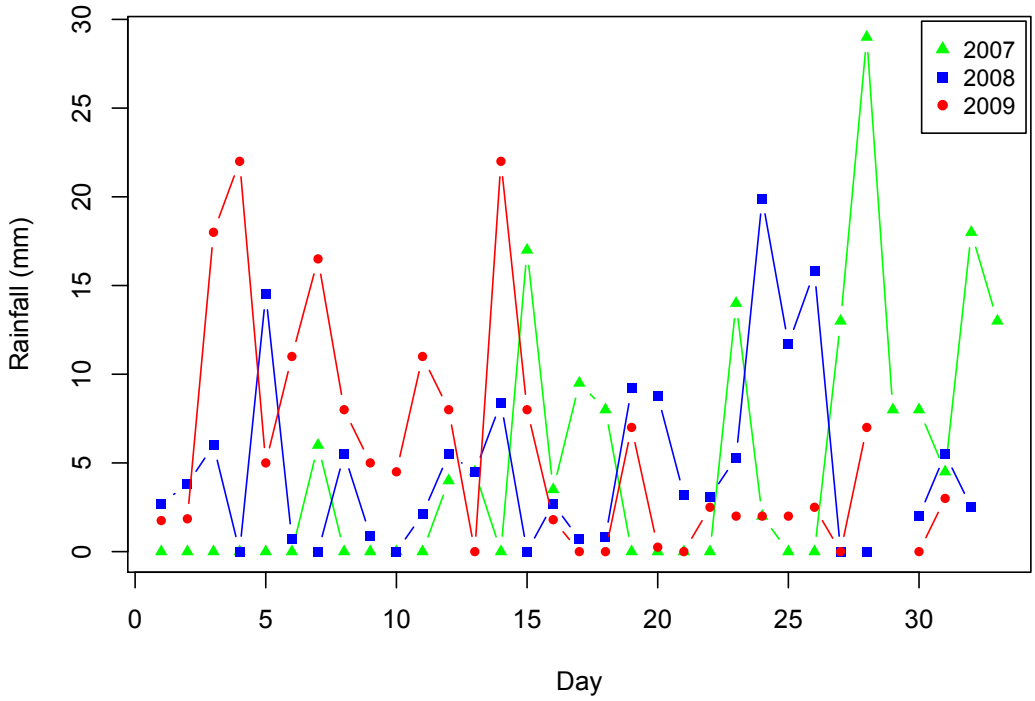


Figure 3.13: The rainfall (mm) for each of the three years. Day 1 = 30th September in each year. Where data are missing no data point is plotted. The legend for each of the years is shown in the top right corner of the figure.

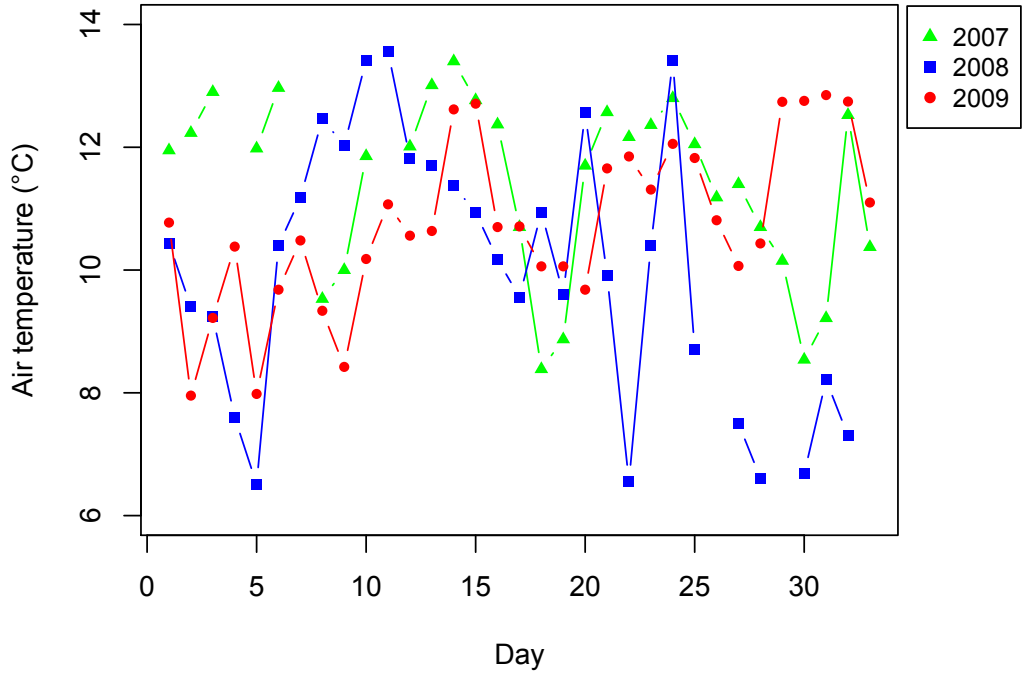


Figure 3.14: The air temperature (°C) for each of the three years. Day 1 = 30th September in each year. Where data are missing no data point is plotted. The legend for each of the years is shown in the top right. The data are the mean of the air temperature for a given day. The plot only uses data for the hours in which behavioural observations were carried out on the given day.

max. r = 0.19, $p < 0.001$), but not in 2007 (r = 0.066, $p = 0.219$; r = 0.093, $p = 0.018$; r = 0.077, $p = 0.055$). Therefore, an increase in rainfall resulted in females being further away from pools of water, and as a consequence, the density of females (within a 10 m buffer zone) decreased. Furthermore, air temperature had a strongly significant, negative relationship with the distance to the nearest pool in 2007 and 2008 (min. r = -0.185, max. r = -0.242, $p < 0.001$, n = 6). Therefore, during these breeding seasons, the higher the air temperature was, the closer the females were to a pool of water, which does support the supposition that pools of water are important for thermoregulation (Twiss et al., 2000; Redman et al., 2001). However, the same pattern was not seen in the 2009 re-sighted individuals' datasets (r = -0.031, $p = 0.385$; r = 0.068, $p = 0.009$; r = -0.073, $p = 0.03$).

Interestingly, in 2009 there was a greater amount of rainfall coupled with lower air temperatures during the first 12 to 15 days of the breeding season, compared to 2007 and 2008 (Figures 3.13 and 3.14). This variation in the weather covariates between breeding seasons may explain why the relationship between the air temperature and the distance to the nearest pool was not apparent in the 2009 datasets. In other words, the increase in rainfall and the reduced air temperature at the beginning of the breeding season may have played an influential role in disrupting what was a strongly significant relationship in the 2007 and 2008 breeding seasons. These findings continue to raise interesting questions with respect to the casual relationship between seals' behaviour and air temperature, rainfall and access to pools of water (Twiss et al., 2000; Redman et al., 2001). It may be that rainfall and air temperature do play a direct, influential role in thermoregulation and/or an individual's requirement to maintain a positive water balance (Twiss et al., 2000; Redman et al., 2001). For example, lower air temperatures may reduce an individual's core temperature, whereas increased rainfall results in more small, localised pools (puddles) of water that may be adequate for individuals to drink from (which has been regularly observed on North Rona, Culloch, Pomeroy & Twiss, pers. obs.; however, whether or not this behaviour relates to maintaining a positive water balance remains unknown). Nevertheless, irrespective of the causal relationship, these data further suggest that air temperature and (perhaps more so) rainfall are influential covariates with respects to the behaviour and the distribution of seals on the breeding colony.

Several other patterns in the re-sighted individuals' datasets reinforce the supposition that the weather covariates and the availability of pools do influence behaviour. For example, there was a significantly negative relationship between the age of the pup and the distance between the mother and her pup in the 2007 and 2008 breeding seasons (min. r = -0.172, max. r = -0.229, $p < 0.001$, n = 6). Therefore, the older the pup was, the closer it was to its mother which might be expected, given that older pups are more physically able to follow their mothers; however, this relationship was not as evident in 2009. This may have been a product of the increased rainfall and lower air temperatures, which meant that females had a reduced need to commute to pools, and as a consequence could stay closer to their pup during the early stages of lactation. Furthermore, the more favourable conditions in 2009 may have influenced other correlations between covariates. For example, in 2007 and 2008, the closer a mother was to the centre of the core area of her home range, the closer she was to her pup (min. r = -0.167, max. r = -0.27, $p < 0.001$, n = 6) and the closer a female was to a pool of water, the closer she was to her nearest female neighbour (min. r = 0.107, max. r = 0.313, min. $p < 0.001$, max. $p = 0.01$, n = 6). Therefore, the increased rainfall and lower air temperatures at the beginning of the 2009 breeding season appears to have reduced a female's need to commute in order to access pools of water and, as a consequence, has minimised the potential cost of permanent mother–pup separation (Redman et al., 2001).

The age of the pup was collinear with the mothers' home range usage. In all 9 analyses the correlation had a strongly significant, positive relationship (min. r = 0.12, max. r = 0.38, $p < 0.001$, n = 9). Therefore, the younger the pup was, the further the mother was from the core area of her home range. This supports the supposition that females, in general, pup further from a pool, in a comparatively lower density area, and as the pup becomes older and therefore less vulnerable (Anderson et al., 1979), the mother shifts her area of activity (home range) closer to a pool. Then, as discussed above, as the pup gets older it moves with its mother (although there was no consistent correlation to suggest that the older the pup was, the closer it was to a pool). As expected, this shift in habitat use coincides with the reduced percentage of time spent in the locomotion behavioural category as the day's postpartum increase, which has also been shown in other

studies (Boness & James, 1979). Therefore, these data support the pup-pool trade-off described by Redman et al. (2001), but also suggest that the shift in the trade-off between pup and pool is related, in part, to the age of the pup.

Although there is no evidence that pup mortality is related to local density (Twiss et al., 2003), it is likely that a mother, particularly when her pup is younger and more vulnerable (Anderson et al., 1979), would rather leave the pup than have it commute with her to a high density area where there is likely to be an increased level of movement by conspecifics (Redman et al., 2001). However, pup mortality is at its highest at the access points to the colony (gullies leading to and from the sea) where there is a high volume of movement by adults (Twiss et al., 2003). Therefore, it may be that a similar pattern is shown in the present study, but on a finer spatial scale. Specifically, mothers may give birth in low density areas where few individuals commute to and from as a mechanism to minimise pup mortality. If this is the case, then this does raise some interesting questions with respect to potential threats to pups from gulls (Twiss et al., 2003) and (on terrestrial colonies) foxes (Culloch et al., 2012).

The significant correlations between the age of the pup and the rainfall, and the age of the pup and the air temperature are most likely due to temporal effects. These relationships are positive and negative, respectively, with the exception of the 2009 breeding season where the analyses of all three re-sighted individuals' datasets produced the opposite result. The temporal effect relates to the peak of the breeding season, which occurs between 8th - 10th October (Hewer, 1959; Hiby et al., 1996; Twiss et al., 2000). Therefore, there are more pups being born in the earlier part of the breeding season when it is typically warmer (Figure 3.14) and, later in the breeding season, when the pups are generally older, there is typically more rainfall (Figure 3.13). However, for the 2009 breeding season, the converse was true; there was more rainfall during the early and mid section of the breeding season and it was also, on average, warmer towards the latter stages of the 2009 breeding season. Therefore, these patterns in air temperature and rainfall would explain the somewhat unexpected correlations between these particular covariates in the 2009 re-sighted individuals' datasets.

There was a significant, negative relationship between the activity of the pup and the home range metric for the 2008 and 2009 re-sighted individuals' datasets (min. r = -0.083, max. r = -0.114, min. $p < 0.001$, max. $p = 0.004$, n = 6). Therefore, pups were less active the closer their mother was to the centre of the core area of her home range. However, there is no consistent relationship between the home range usage and the distance the female is to her pup in the 2008 and 2009 breeding seasons. In other words, the mothers' location within her home range is not related to the location of her pup. Consequently, there is no obvious reason as to why the mothers' location would influence the pup's behaviour, which suggests that this correlation is spurious.

The in-depth examination of the collinearity of the covariates has shown that there are important biological relationships in the data, and that these relationships are heavily influenced by the relationship between rainfall, air temperature and availability of pools. However, the influence of collinearity of covariates and the best method for dealing with them in the subsequent analyses is not straightforward (Freckleton, 2011). If collinearity is ignored it can cause extreme biases in the estimated effects of the covariates (Freckleton, 2011). Conversely, if collinear covariates are eliminated without due consideration of their independent effects, then this too could lead to biases in the estimated effect of the covariates (Freckleton, 2011). In the present study, although certain collinear covariates are likely to have independent effects despite collinearity, it was decided that one of each pair of consistently collinear covariates (those that were collinear across all 9 of the re-sighted individuals' datasets) would be dropped from the dataset prior to the analyses presented in Chapters 5 and 6. This approach (of omitting collinear covariates) has the advantage of reducing the risk of a type II error (incorrectly accepting the null hypothesis; Zuur et al., 2009a, b; Freckleton, 2011).

As a result, the distance between the mother and her pup was omitted from the analyses in favour of the distance between the mother and the nearest pool. This has the advantage of increasing the size of the datasets analysed because the distance to the pup was not always known (as a result of the pup being out of sight during mapping). Density was consistently collinear with several covariates

that were not consistently collinear with one another; therefore, density was omitted from the set of covariates used in the subsequent analyses. Given that the age of the pup and the home range metric were strongly collinear, it was decided that pup age should be omitted because the age of some of the pups was an estimate (n = 5). Further justification of this approach is that all of the collinear covariates that were omitted from the analyses had a highly significant ($p < 0.001$) relationship with at least one of the covariates that was retained. After these covariates were omitted the collinearity of the covariates were not reanalysed because the sample size of the data sets did not increase considerably (as a result of omitting the distance between a mother and her pup). Despite omitting covariates that were collinear across all 9 re-sighted individuals' datasets, there was still a considerable amount of collinearity that varied between datasets. This shall be addressed in the relevant sections in Chapters 5 and 6.

3.15. Discussion

The exploratory analyses presented in this chapter are a very important prerequisite to the analyses presented in the subsequent chapters. Although the analyses in the following chapters only include data from re-sighted individuals, the analyses of the gross dataset was important for a number of reasons: 1) these data gave an overview of the average postpartum female grey seals' behaviour whilst on the breeding colony, 2) they assisted in identifying which covariates should be included in the exploratory analyses of the fine-scale datasets, 3) where relevant, they assisted in the rationale of which covariates should be included in the models presented in the subsequent chapters, 4) where relevant, they assisted in the interpretation of the model output presented in the following chapters.

Chapter Four:
Do consistent individual differences in behaviour occur in postpartum female grey seals across breeding seasons?

4.1. Introduction

As noted in Chapter 1, consistent individual differences (CIDs) in behaviour has gained a lot of interest within the fields of evolutionary and behavioural ecology over the last five to ten years (Sih et al., 2004; Bell, 2007; Dingemanse et al., 2010; Réale et al., 2010; Chapter 1, Figure 1.2). This interest has grown exponentially due to the fundamental principal that if individuals do behave consistently across time, situations (defined as different ecological conditions, e.g. different levels of predation risk) and/or contexts (defined as a functional behavioural category, e.g. feeding, mating or parental care) then this suggests that an individual's behavioural plasticity is (to some degree) constrained (Wilson, 1998; Bell & Stamps, 2004; Dall et al., 2004; Réale et al., 2010). Consequently, this raises important questions about the potential impacts of CIDs in behaviour in relation to: adaptation to rapid environmental changes including climate change (e.g. Réale et al., 2003; Dingemanse et al., 2004), genetic diversity (e.g. Dingemanse et al., 2002; van Ores et al., 2004), fitness (e.g. Dingemanse et al., 2004; Dingemanse & Réale, 2005; Alvarez & Bell, 2007; Smith & Blumstein, 2008), population dynamics (e.g. Bell, 2005; Dingemanse et al., 2007) welfare (e.g. Huntingford & Adams, 2005; Muller & Schrader, 2005; Huntingford, 2007) and conservation and management practices (e.g. Blumstein et al., 2006; McDougall et al., 2006). More recently, researchers have acknowledged that to fully understand the ecological and evolutionary implications of CIDs in behaviour, it is important that future studies attempt to quantify whether or not these behavioural patterns occur in the natural environment (e.g. Bell, 2005; Dingemanse & Réale, 2005; Archard & Braithwaite, 2010).

4.2. The definition of 'consistency'

Throughout this thesis, the terms (and derivatives of the terms), 'consistency' and 'repeatability' shall be used interchangeably and will be

considered synonymous. This terminology follows that of other researchers working in this field of evolutionary and behavioural ecology (e.g. Hayes & Jenkins, 1997; Bell et al., 2009). Repeatability is defined as the proportion of behavioural variation that is due to differences between individuals (Lessells & Boag, 1987; Boake, 1989; Hayes & Jenkins, 1997; Bell et al., 2009). It is a function of both within-individual variance and between-individual variance. Repeatability can be low for two reasons: high within-individual variance or low between-individual variance. Behaviours that show relatively low within-individual variance combined with high between-individual variance are more repeatable. In other words, the more consistent an individual behaves through time and the greater the difference between individuals' behaviour within the group or population, then the more repeatable the behaviour is (Hayes & Jenkins, 1997; Bell et al., 2009).

4.3. Statistical analysis of repeatability

The most suitable and most widely used statistic for estimating repeatability is the Intraclass Correlation Coefficient (ICC), which is specifically designed to test the relationship among variables that share both their metric and their variance (Shrout & Fleiss, 1979; McGraw & Wong, 1996). The ICC ranges between 0 and 1, where 0 indicates that all the variation is within individuals (i.e. the means of the repeated measures for all individuals are equal) and 1, which indicates that all the variation is between individuals (i.e. every time an individual is measured the same value is obtained; Hayes & Jenkins, 1997). There are three commonly used single measure models, often referred to as ICC1, ICC2 and ICC3 (Shrout & Fleiss, 1979; Table 4.1). ICC1 is a one-way model, which assumes that the rows (individuals) are the only systematic source of variation. ICC2 and ICC3 are two-way models, where the columns (the repeated measures) are considered as random or fixed-effects, respectively. Statistically speaking, this means that for ICC2 the column variance is included in the denominator variance, whereas for ICC3, it is excluded. Therefore, by using the ICC3, the column variance is deemed to be an irrelevant source of variance (McGraw & Wong, 1996). From a biological perspective it is likely that column variance would be a relevant source of variation. For example, consider a scenario where a researcher wants to determine the repeatability of a behaviour for three individuals (rows) across two separate

occasions (columns) by counting the number of times behaviour *x* occurs in one hour. On the first occasion the researcher counts 20, 40 and 60 occurrences for individuals 1, 2 and 3, respectively. Whilst on the second occasion the researcher counts 40, 60 and 80 occurrences for individuals 1, 2 and 3, respectively. ICC analyses of these data would show that ICC3 gives a perfect correlation (1.00). Therefore, by excluding column variance it does not matter that the counts were lower on the first occasion, because the counts agree to the extent that an additive transformation serves to equate them (i.e. subtracting the mean count for both occasions from the individual counts given; this would equate to 20, 0, -20 for both occasions and therefore a perfect correlation). However, the variation in behaviour between the two time points is likely to be biologically relevant and/or of interest. Consequently, by using ICC2 the correlation is not perfect (0.67), because the counts differ considerably in their absolute value, and are therefore viewed as 'disagreements'.

Table 4.1: The Intraclass Correlation Coefficients (ICC) for single measure models, the table gives the name of the ICC, the structure of the model and the description of the model. Following the terminology in the literature, columns are referred to as 'judges' and rows are referred to as 'targets' (Shrout & Fleiss, 1979 and McGraw & Wong, 1996).

ICC	Structure of Model	Description of Model
ICC1	$\frac{MSB - MSW}{MSB + (k-1)MSW}$	One way ANOVA fixed-effects model
ICC2	$\frac{MSB - MSE}{MSB + (k-1)MSE + k(MSJ - MSE)/n}$	Random sample of judges rate each target. The measure is one of absolute agreement in the ratings
ICC3	$\frac{MSB - MSE}{MSB + (k-1)MSE}$	Fixed sample of judges rate each target. There is no generalisation to a larger population of judges

MSB = variance between targets; MSW = variance within targets; MSE = variance due to the interaction of judge by target; MSJ = variance due to the judges; k = number of judges; n = number of targets

If a Pearson product-moment or the Spearman's rank correlation coefficients were used on the same dataset it would give the same result as the ICC3 analysis. However, these correlation coefficients are better suited for measurements that do not share their variance or their metric, which is why they are occasionally referred to as *Inter*class Correlation Coefficients (McGraw & Wong, 1996; Bell et al., 2009). The principal distinction between the ICC and the Interclass Correlation Coefficient are that the former uses an additivity index, which (in the case of 2 occasions (columns)) measures the degree to which one variable (y) can be equated to another variable (x) by adding a constant ($y = x +$ b). Conversely, the Interclass Correlation Coefficient uses a linear index, which measures the degree to which one variable (y) can be equated to another variable (x) by a linear transformation ($y = ax +$ b) (McGraw & Wong, 1996). The importance of correctly selecting between the additivity and the linear index can be simply demonstrated; for example, consider three paired scores (10,14), (15,15) and (20,16). Both Interclass Correlation Coefficients consider these scores to be in perfect agreement (1.00), where ICC3 does not (0.38). Therefore, in order to select the correct statistical test (and consequently, obtain the correct result), it is important to differentiate between variables that share their metric and variance (ICC) and those that do not (Interclass Correlation Coefficient). An additional benefit of the ICC is that it can be used to analyse as many columns of data as there are available.

The repeatability estimate of an ICC is the property of the population of individuals and gives little information about whether specific individuals are themselves repeatable (Hayes & Jenkins, 1997; Bell et al., 2009). Consequently, even if the ICC estimate is greater than zero it does not mean that all individuals within the group or population have behaved equally consistently, and given that individuals are likely to differ in how much their behaviour changes between observations, it is unlikely that an ICC will return a perfect repeatability estimate. Conversely, it is possible for the repeatability estimate to fall outside its theoretical limits and have a negative value (indicating that the best estimate for repeatability is zero), which can occur if the variance components have large sampling errors (Hayes & Jenkins, 1997; Bell et al., 2009). There is no rule of thumb as to what constitutes a low or high repeatability estimate, with much of the interpretation

coming from all aspects of the ICC output. This is particularly true of the *p* value, where previous studies have only considered repeatability estimates if $p \leq 0.05$ (e.g. Hayes et al., 1998; Blumstein & Munos, 2005; Cummings & Mollaghan, 2006; Lu et al., 2007; Szafranska et al., 2007; Witsenburg et al., 2010).

4.4. Aims

This chapter will determine whether or not CIDs in any of the eight behavioural categories (Chapter 2, Section 2.5.3) occurred across two or more breeding seasons, which could be regarded as different situations (given that the social and physical environment are likely to vary between breeding seasons; Chapter 3, Section 3.14). The analyses will address how robust repeatability of behaviour is by ascertaining whether or not CIDs in behaviour are maintained, irrespective of which individuals and/or breeding seasons are included in the analyses. Of those behavioural categories that are repeatable, site fidelity measures will be used to ascertain whether or not the environment that the individuals' were experiencing could, in part, account for the repeatability of behaviour.

4.5. Methodology

The data used in this chapter were collected over three consecutive breeding seasons (2007, 2008 and 2009) at the North Study Area (NSA) on North Rona (Chapter 2, Section 2.3.2). This study was entirely observational and despite a number of ongoing long-term studies involving known females on North Rona (Chapter 2, Section 2.3.1), none of the seals within the NSA were handled during the course of this study. This 'hands-off' approach ensured that the seals were observed in as natural an environment as possible with minimal anthropogenic disturbance.

4.5.1. Data selection

Using each individual's gross activity budget (Chapter 3, Section 3.5) the repeatability of all eight of the behavioural categories was estimated across

breeding seasons for all re-sighted postpartum females. Given that the behaviour of the female could have been influenced by the age of her pup and her 'behavioural context' (meaning the rapid transition from maternal care to mating, weaning the pup and leaving the colony), the lactation periods presented in Chapter 3, Section 3.6 were reanalysed for re-sighted individuals only. Each of the breeding seasons was analysed separately, and if there was a significant difference between the lactation periods of a given behavioural category for any of the three breeding seasons, then only the data from the mid-lactation period (where the majority of the data are) was used in the ICC analyses.

4.5.2. Environment variation across breeding seasons

Quantifying the influence of environmental variation on the repeatability of behaviour is fundamentally important if we are to successfully interpret the ecological and evolutionary implications of CIDs in behaviour (Dingemanse et al., 2002; Martin & Réale, 2008a, b; Ellenberg et al., 2009). Given that female grey seals are known to be highly site faithful (Pomeroy et al., 1994; Pomeroy et al., 2005) and show little variation in their pupping date between breeding seasons (Pomeroy et al., 1999), it is feasible that individuals could be experiencing similar social and environmental conditions across breeding seasons (Chapter 2, Section 2.2.2). Therefore, if the fine-scale environment influences behavioural patterns, then higher repeatability estimates may be expected to coincide with a higher degree of site fidelity.

As a preliminary examination of this, two site fidelity metrics were used: the distance between an individual's pupping site between breeding seasons and the distance between the centre of the core area of an individual's home range between breeding seasons (see Chapter 2, Section 2.5.5 for details on how these data were collected and Chapter 2, Section 2.5.6 for details on how these data were derived). Both site fidelity metrics were included in these analyses because they are likely to have different biological implications with reference to habitat selection and habitat use. For example, both the pupping site and the centre of the core area of the home range may be influenced by environmental conditions (e.g. availability of pools; Redman et al., 2001), whilst the latter may also be influenced

by environmental variation during lactation, which may also include the behaviour of the mothers' pup and/or conspecifics (Chapter 3, Sections 3.8.1 and 3.10).

Quantifying the influence of site fidelity on behaviour was only carried out on pairwise breeding seasons where the ICC analysis yielded a significant repeatability estimate. If these criteria were met, then these site fidelity metrics were used as a proxy to assess whether or not habitat selection and/or habitat use influenced the repeatability of behaviour. If the CIDs in behaviour persisted after accounting for this environmental variation, then this suggests that the repeatability may be a product of the group of individuals and not the environment they were experiencing. In other words, repeatability of behaviour could be influenced by intrinsic (rather than extrinsic) factors that are inherent to the individuals that form the group. These intrinsic factors may include previous experience, age, state and/or condition (e.g. Réale & Festa-Bianchet, 2003; Ellenberg, et al., 2009; Réale et al., 2010; Stamps & Groothuis, 2010a, b).

If the repeatability estimate was significant, then a linear regression of the proportion of time spent in the given behavioural category across the two breeding seasons was carried out. This was done such that the behavioural data from the earlier breeding season was used as the independent (x-axis) variable and the behavioural data from the subsequent breeding season was used as the dependent (y-axis) variable. The absolute values for the residuals from the linear regression were extracted and plotted against the site fidelity measures (this is often referred to as a partial regression plot; Zuur et al., 2007). The absolute residuals were used in the partial regression plots because a high degree of site fidelity would be expected to correspond to a low residual value (irrespective of whether or not it was positive or negative). In other words, individuals that were highly site faithful would be expected to show little variation in their behaviour between breeding seasons. To ascertain whether or not there was a significant correlation between the absolute residuals and the degree of site fidelity, the Spearman's rank correlation coefficient was used.

4.5.3. Repeatability analyses

An ICC two-way model was used to ascertain whether or not CIDs in behaviour occurred between re-sighted individuals. A two-way model was selected because the breeding seasons (columns) and the individual females (rows) have a systematic source of variance associated with them (Table 4.1). The data in each row was the proportion of time that the re-sighted individual spent in the given behavioural category over the course of their time on the breeding colony, postpartum. The results presented in this chapter are taken from ICC2, which means that the variation in the individual's behaviour between breeding seasons is included in the model (McGraw & Wong, 1996). For each of the behavioural categories, all pairwise analyses of breeding seasons (2007 & 2008; 2008 & 2009; 2007 & 2009) and the analysis of the three consecutive breeding seasons (2007 - 2009) were carried out. Therefore, for each of the behavioural categories there were a total of four analyses. All results giving a significant *p* value (≤ 0.05) are considered repeatable. All of the significant repeatability estimates are plotted. In order to prevent repetition, where the same plots of different data are presented, a legend describing all of the figures shall be provided prior to presenting the figures. ICC analyses were carried out using the ICC() function in the R package *psych* (Revelle, 2011).

4.6. Results

There were 8 known individuals re-sighted in all three years, 8 additional known individuals were re-sighted in two consecutive years, and one known individual was re-sighted after skipping a year (not seen in 2008; Chapter 3, Section 3.9). As a consequence of the lactation period analyses, the pup check, locomotion, presenting & nursing and pup interactions behavioural categories used data from the mid-lactation period only, whilst the resting, comfort move, alert and aggression behavioural categories used data from all three lactation periods (Table A4.1). To clarify the terms used hereafter; repeatability refers to the repeatability estimates, whereas the term robust refers to the number of analyses in which the behaviour was significantly repeatable. For example, it is possible to

have a behaviour that is highly repeatable but is not robust (e.g. if only one of the four analyses had a significant ICC with a high repeatability estimate).

4.6.1. CIDs in the behaviour of postpartum female grey seals

Repeatability occurred in five of the eight behavioural categories (Table 4.2). Alert was the only behavioural category that was repeatable in all four analyses; conversely, the resting, comfort movement and locomotion behavioural categories were not repeatable in any of the analyses. The significant repeatability estimates ranged from 0.39 to 0.82 across all behavioural categories in all four analyses (Table 4.2; Figures 4.1 - 4.12). The repeatability estimates of ICC3 were similar to those of ICC2 (Table A4.2), which suggests that there was little systematic change in individuals' behaviour across breeding seasons. As an indication of behavioural plasticity between breeding seasons, the 1:1 line and the line of best fit was included in all pairwise plots (Figures 4.1, 4.3 - 4.5, 4.7 - 4.9, 4.11 and 4.12). In some cases, the line of best fit is clearly influenced by widespread and/or outlying data points (e.g. Figures 4.8, 4.11 and 4.12). Consequently, there are some individuals that are considerably influencing the outcome of the analyses; for example, if 907 is omitted from Figure 4.11 (aggression, 2007 & 2008) and from Figure 4.12 (aggression, 2008 & 2009) the ICCs are no longer significant (ICC2 = 0.13, F = 1.3, p = 0.38; ICC2 = 0.17, F = 1.5, p = 0.29, respectively). The plots for the three years (Figures 4.2, 4.6 and 4.10) are harder to visually interpret, as individuals do not always maintain rank order across breeding seasons. Nevertheless, these plots do show a varying degree of consistency between the eight individuals for each of the three behavioural categories.

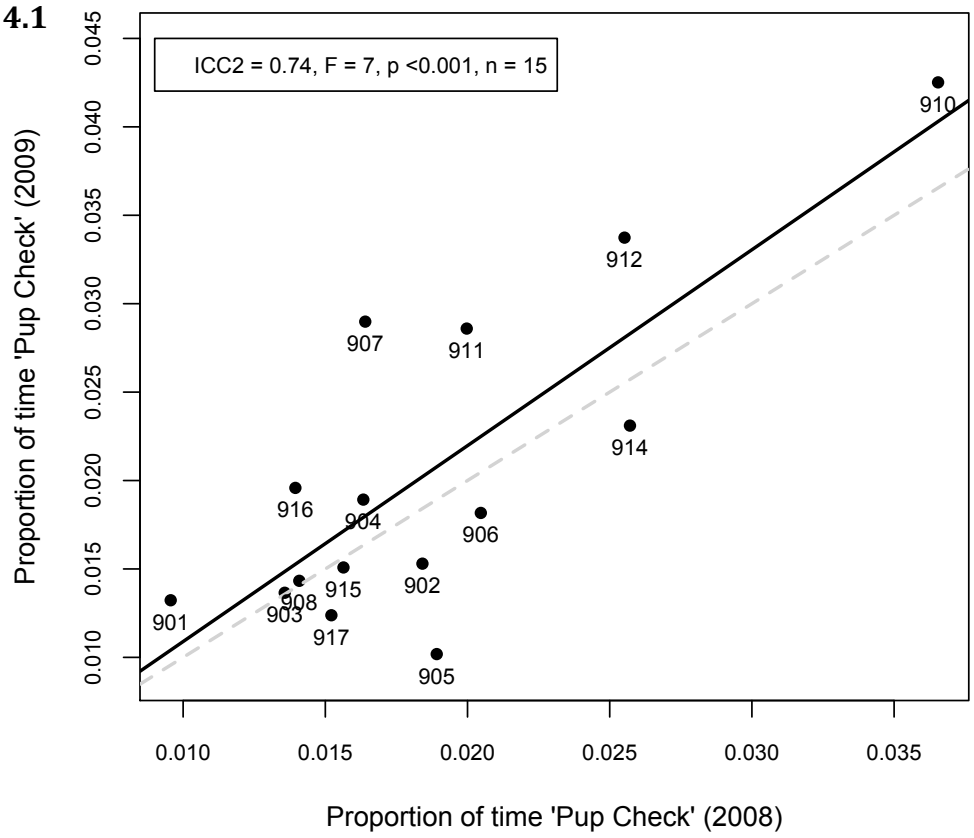
Table 4.2: ICC2 analyses for all 3 years (n = 8), 2007 & 2008 (n = 9), 2008 & 2009 (n = 15), 2007 & 2009 (n = 9), the Lactation Period(s) (LP) used are based on the lactation period analyses (Table A4.1). All significant results are in bold. Where ICC values are negative the best estimate for repeatability is zero (Hayes & Jenkins, 1997; Bell et al., 2009). See Table A4.2 for ICC3 results. The lower and upper columns show the 95% confidence limits.

Behaviour	Years	LP	ICC	F	*p*	lower	upper
Resting	2007 - 2009	ALL	0.137	1.6	0.22	-0.17	0.63
	2007 & 2008	ALL	0.4	2.5	0.11	-0.21	0.81
	2008 & 2009	ALL	0.39	2.2	0.078	-0.17	0.72
	2007 & 2009	ALL	0.30	1.8	0.22	-0.51	0.79
Comfort Movement	2007 - 2009	ALL	-0.071	0.73	0.65	-0.25	0.38
	2007 & 2008	ALL	0.015	1.04	0.48	-0.46	0.6
	2008 & 2009	ALL	-0.22	0.96	0.53	-0.50	0.32
	2007 & 2009	ALL	-0.068	0.86	0.58	-0.57	0.56
Pup Check	2007 - 2009	MID	0.21	1.9	0.14	-0.13	0.68
	2007 & 2008	MID	0.3	1.9	0.19	-0.34	0.77
	2008 & 2009	**MID**	**0.74**	**7.0**	**<0.001**	**0.41**	**0.90**
	2007 & 2009	MID	0.10	1.3	0.37	-0.39	0.65
Alert	**2007 - 2009**	**ALL**	**0.75**	**10.2**	**<0.001**	**0.41**	**0.94**
	2007 & 2008	**ALL**	**0.72**	**6**	**0.01**	**0.19**	**0.93**
	2008 & 2009	**ALL**	**0.67**	**4.7**	**0.003**	**0.24**	**0.87**
	2007 & 2009	**ALL**	**0.82**	**8.8**	**0.003**	**0.36**	**0.96**
Locomotion	2007 - 2009	MID	0.35	2.4	0.078	-0.125	0.79
	2007 & 2008	MID	0.25	1.6	0.26	-0.56	0.77
	2008 & 2009	MID	0.26	1.8	0.15	-0.21	0.65
	2007 & 2009	MID	0.50	2.8	0.084	-0.25	0.86
Presenting & Nursing	**2007 - 2009**	**MID**	**0.39**	**4.1**	**0.012**	**0.018**	**0.79**
	2007 & 2008	MID	0.24	2	0.18	-0.22	0.72
	2008 & 2009	**MID**	**0.52**	**3.2**	**0.02**	**0.042**	**0.80**
	2007 & 2009	MID	0.31	1.9	0.20	-0.42	0.79
Pup Interaction	2007 - 2009	MID	0.13	1.5	0.24	-0.19	0.64
	2007 & 2008	MID	0.17	1.5	0.29	-0.36	0.7
	2008 & 2009	**MID**	**0.58**	**3.7**	**0.01**	**0.12**	**0.81**
	2007 & 2009	**MID**	**0.55**	**4.5**	**0.024**	**-0.046**	**0.87**
Aggression	**2007 - 2009**	**ALL**	**0.53**	**5.0**	**0.005**	**0.124**	**0.86**
	2007 & 2008	**ALL**	**0.65**	**4.5**	**0.024**	**0.036**	**0.91**
	2008 & 2009	**ALL**	**0.48**	**3.6**	**0.011**	**0.005**	**0.78**
	2007 & 2009	ALL	0.14	1.3	0.36	-0.62	0.72

The following 6 pages show:

Figures 4.1 - 4.12: The plots of the significant repeatability estimates for: **4.1**). Pup check (2008 & 2009), **4.2, 4.3**, **4.4**, **4.5**). Alert (2007 - 2009; 2007 & 2008; 2008 & 2009; 2007 & 2009, respectively), **4.6**, **4.7)**. Presenting & nursing (2007 - 2009; 2008 & 2009, respectively) **4.8**, **4.9**). Pup interactions (2008 & 2009; 2007 & 2009, respectively), **4.10**, **4.11**, **4.12**). Aggression (2007 - 2009; 2007 & 2008; 2008 & 2009, respectively). ICC2 results are shown in the legend within each of the plots. For the figures presenting three years' of data the individual ID numbers are shown in the legend out-with the plot and are colour coded to the plotted lines. For the figures presenting two years' of data the individual ID numbers are given for each data point. The line of best fit (black solid line) and the 1:1 line (grey dashed line) are presented in the pairwise plots.

4.1


ICC2 = 0.74, F = 7, p <0.001, n = 15
Proportion of time 'Pup Check' (2009)
Proportion of time 'Pup Check' (2008)
0.010
0.015
0.020
0.025
0.030
0.035
0.040
0.045
901
902
903
904
905
906
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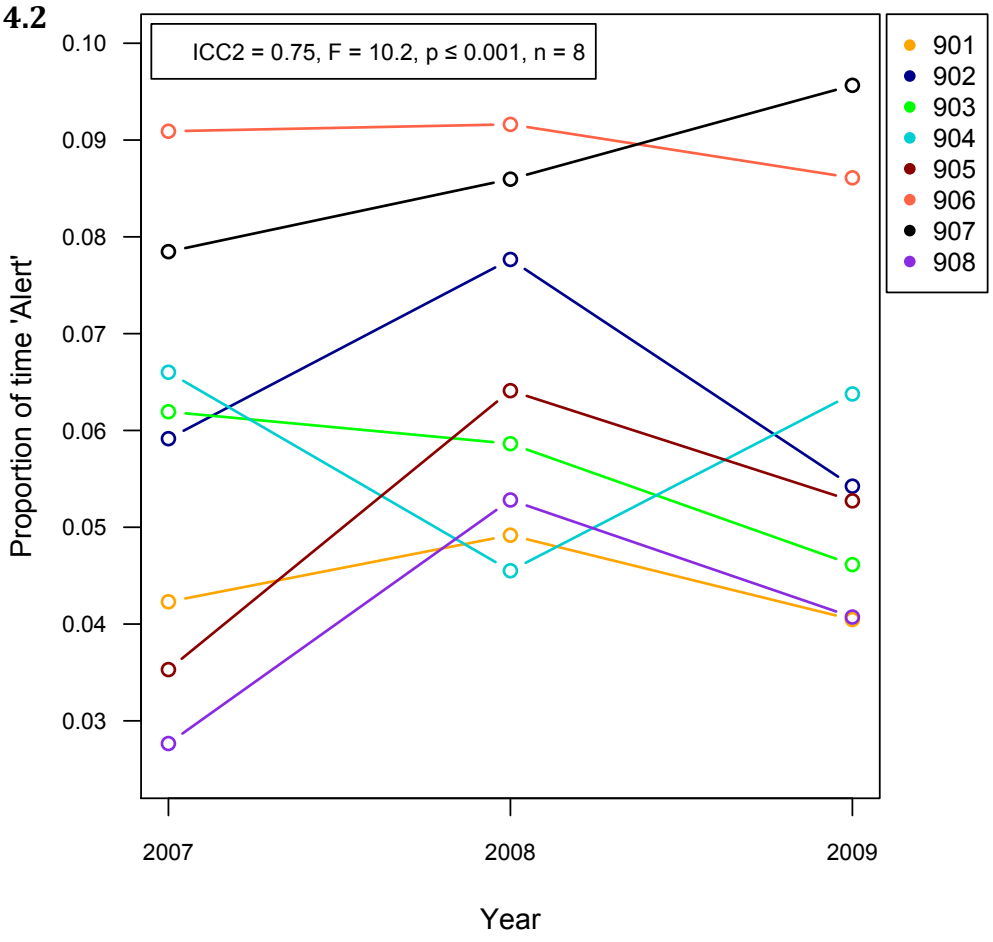
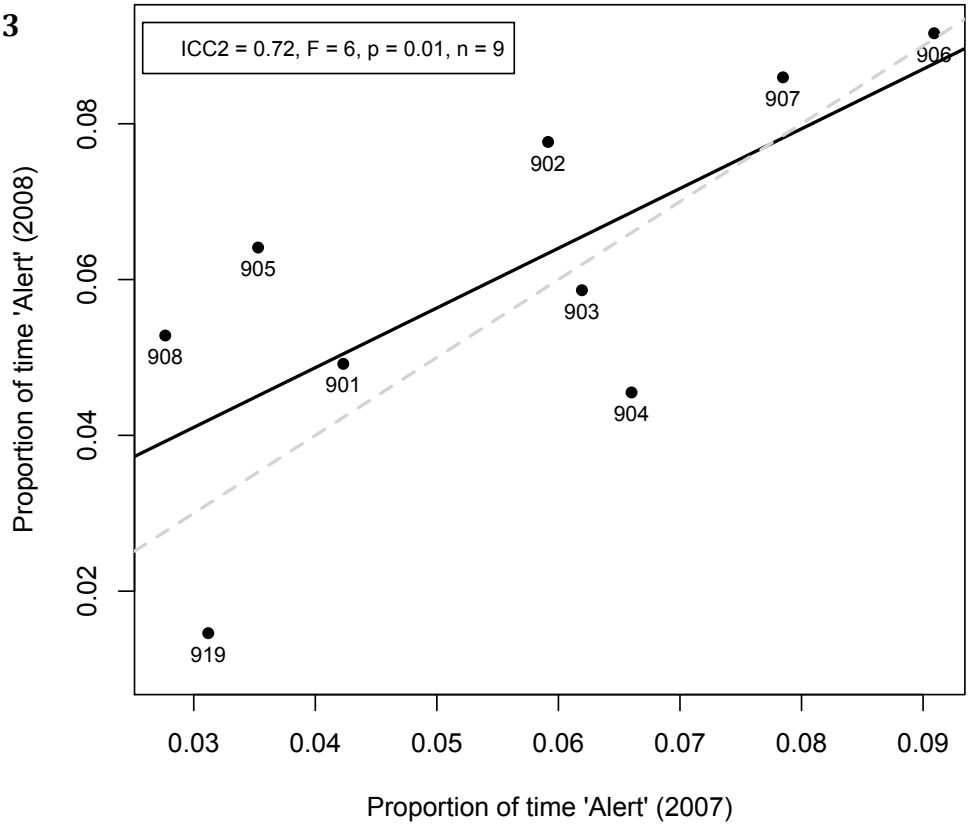
908
910
911
912
914
915
916
917

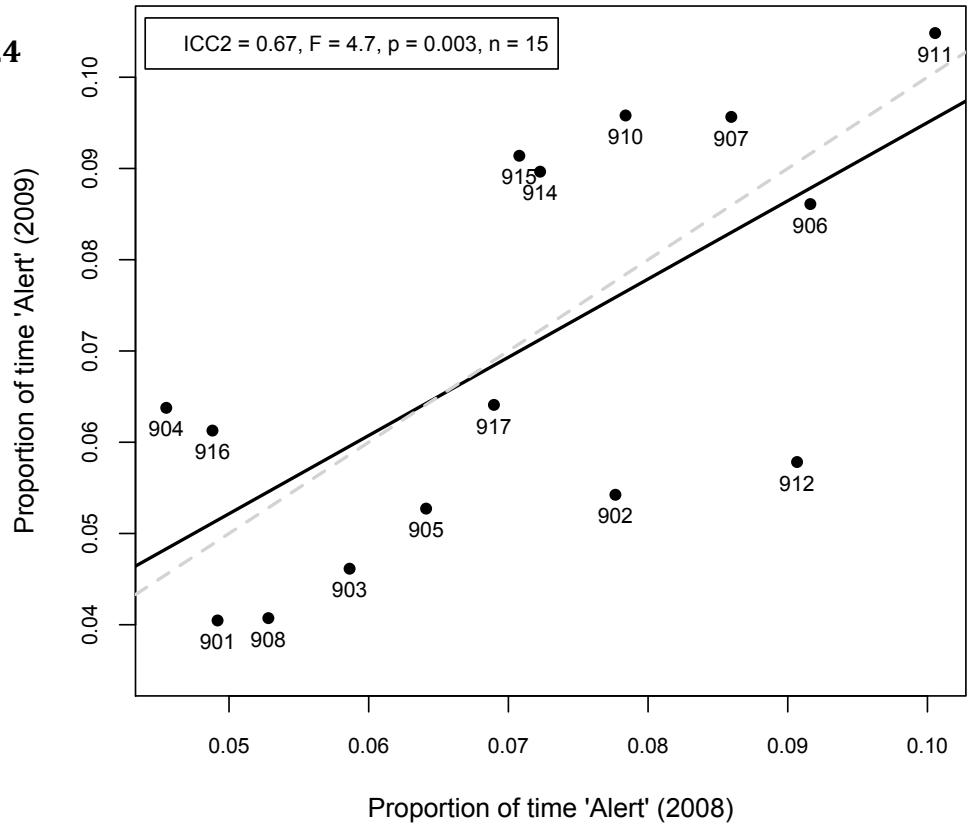
4.2


ICC2 = 0.75, F = 10.2, p ≤ 0.001, n = 8
Proportion of time 'Alert'
Year
0.03
0.04
0.05
0.06
0.07
0.08
0.09
0.10
2007
2008
2009
901
902
903
904
905
906
907
908

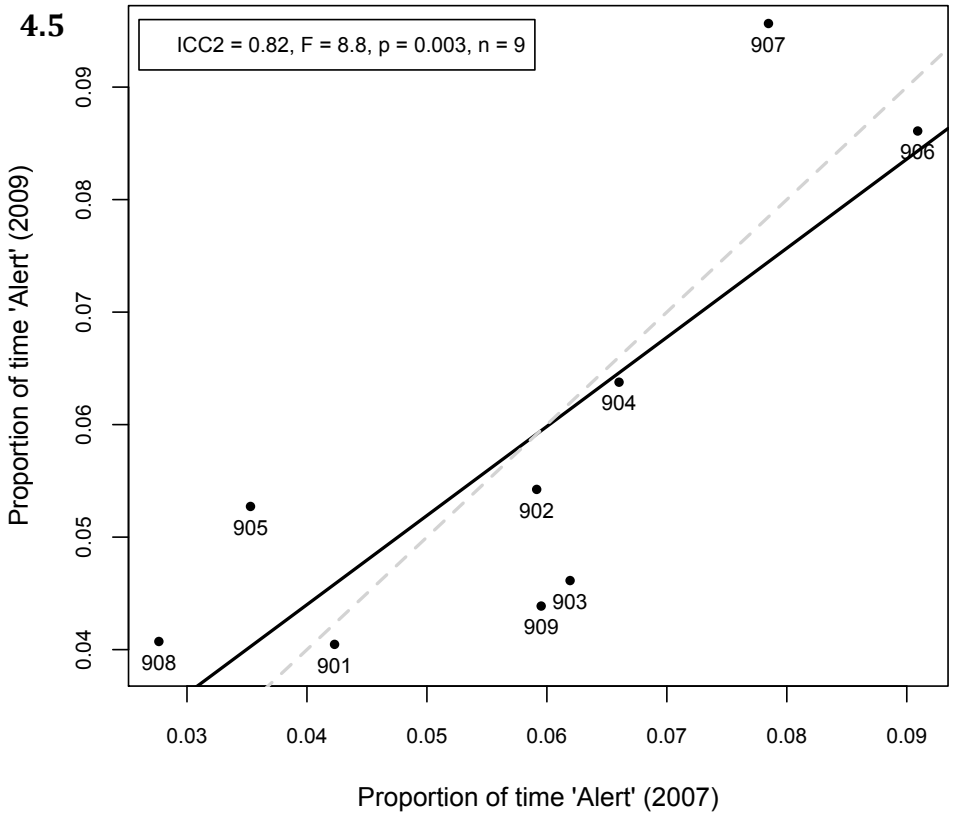
4.3


ICC2 = 0.72, F = 6, p = 0.01, n = 9
Proportion of time 'Alert' (2008)
Proportion of time 'Alert' (2007)
0.02
0.04
0.06
0.08
0.03
0.04
0.05
0.06
0.07
0.08
0.09
906
907
902
905
903
908
901
904
919

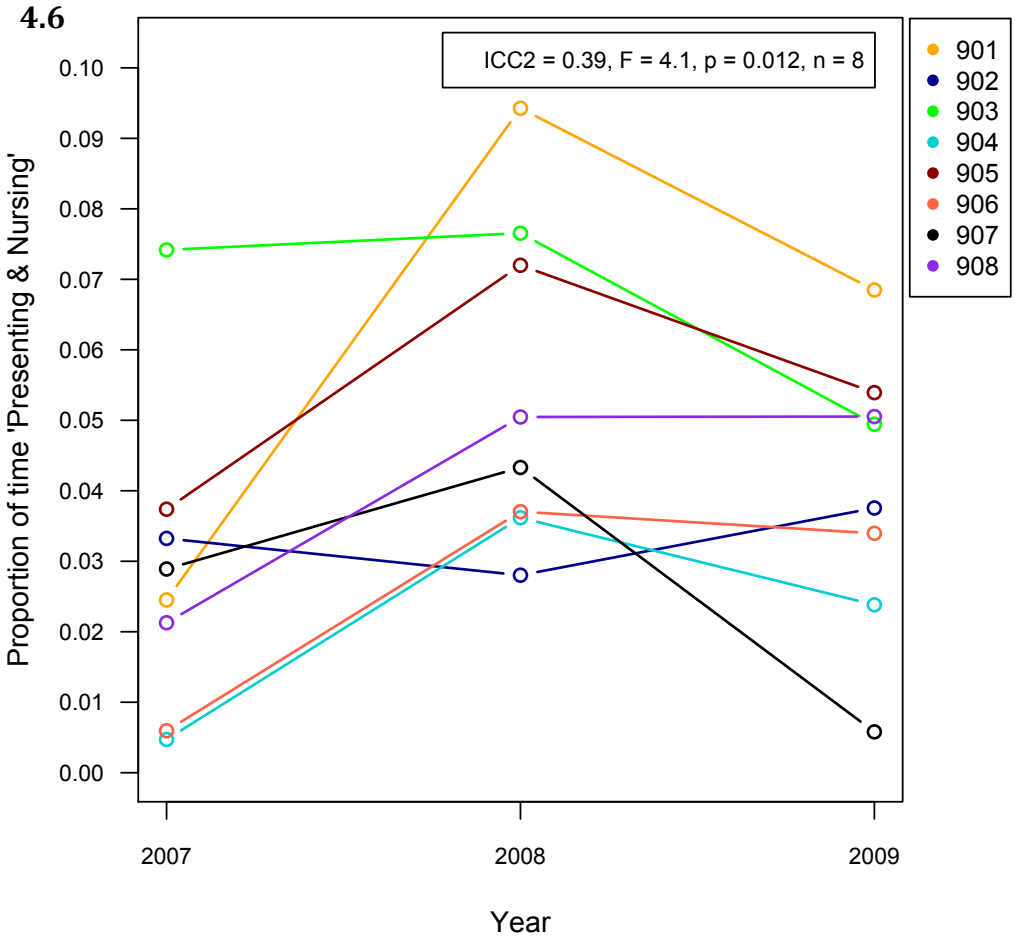
4.4


ICC2 = 0.67, F = 4.7, p = 0.003, n = 15
Proportion of time 'Alert' (2009)
Proportion of time 'Alert' (2008)
0.04
0.05
0.06
0.07
0.08
0.09
0.10
0.05
0.06
0.07
0.08
0.09
0.10
911
910
907
915
914
906
904
916
917
912
905
902
903
901
908

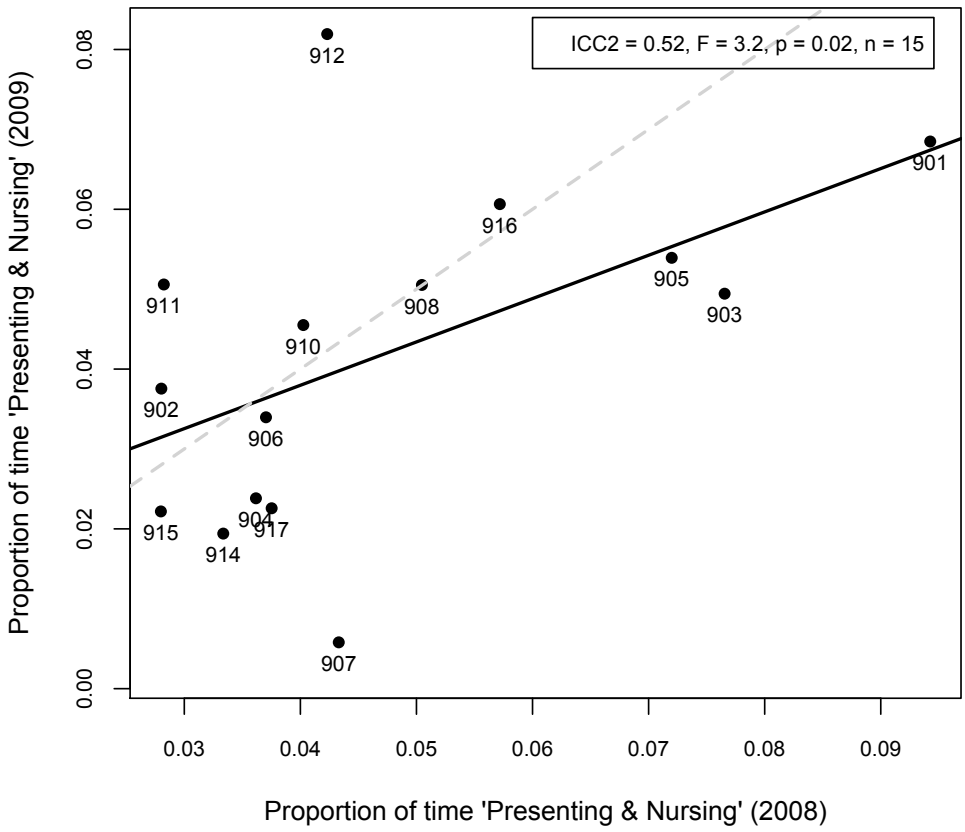
4.5


ICC2 = 0.82, F = 8.8, p = 0.003, n = 9
Proportion of time 'Alert' (2009)
Proportion of time 'Alert' (2007)
0.03
0.04
0.05
0.06
0.07
0.08
0.09
907
906
904
905
902
903
909
908
901

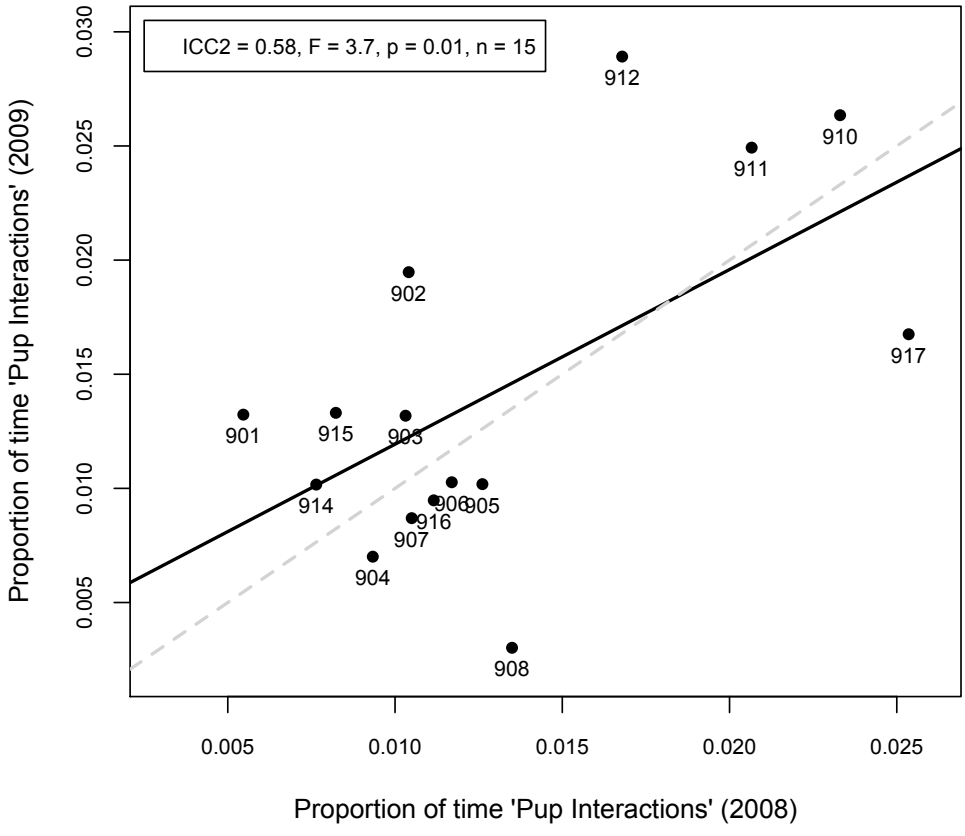
4.6


ICC2 = 0.39, F = 4.1, p = 0.012, n = 8
Proportion of time 'Presenting & Nursing'
Year
2007
2008
2009
0.00
0.01
0.02
0.03
0.04
0.05
0.06
0.07
0.08
0.09
0.10
901
902
903
904
905
906
907
908

4.7


ICC2 = 0.52, F = 3.2, p = 0.02, n = 15
Proportion of time 'Presenting & Nursing' (2009)
Proportion of time 'Presenting & Nursing' (2008)
0.00
0.02
0.04
0.06
0.08
0.03
0.04
0.05
0.06
0.07
0.08
0.09
912
901
916
905
911
908
903
910
902
906
915
904
917
914
907

4.8


ICC2 = 0.58, F = 3.7, p = 0.01, n = 15
Proportion of time 'Pup Interactions' (2009)
Proportion of time 'Pup Interactions' (2008)
0.005
0.010
0.015
0.020
0.025
0.030
0.005
0.010
0.015
0.020
0.025
912
910
911
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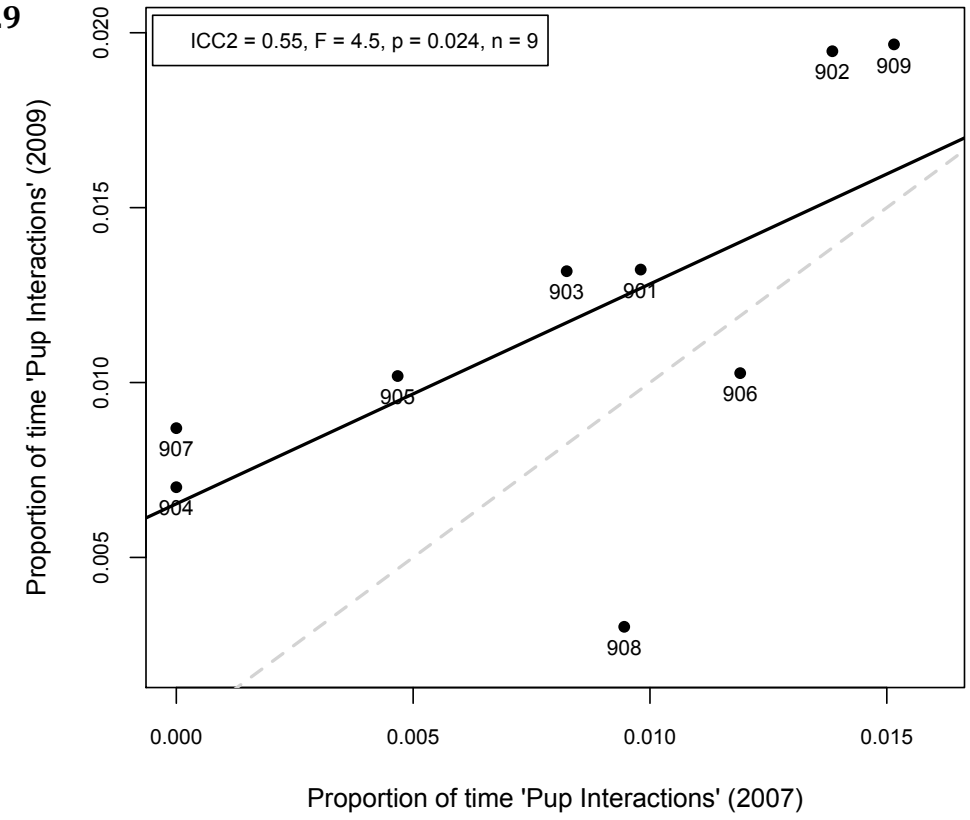
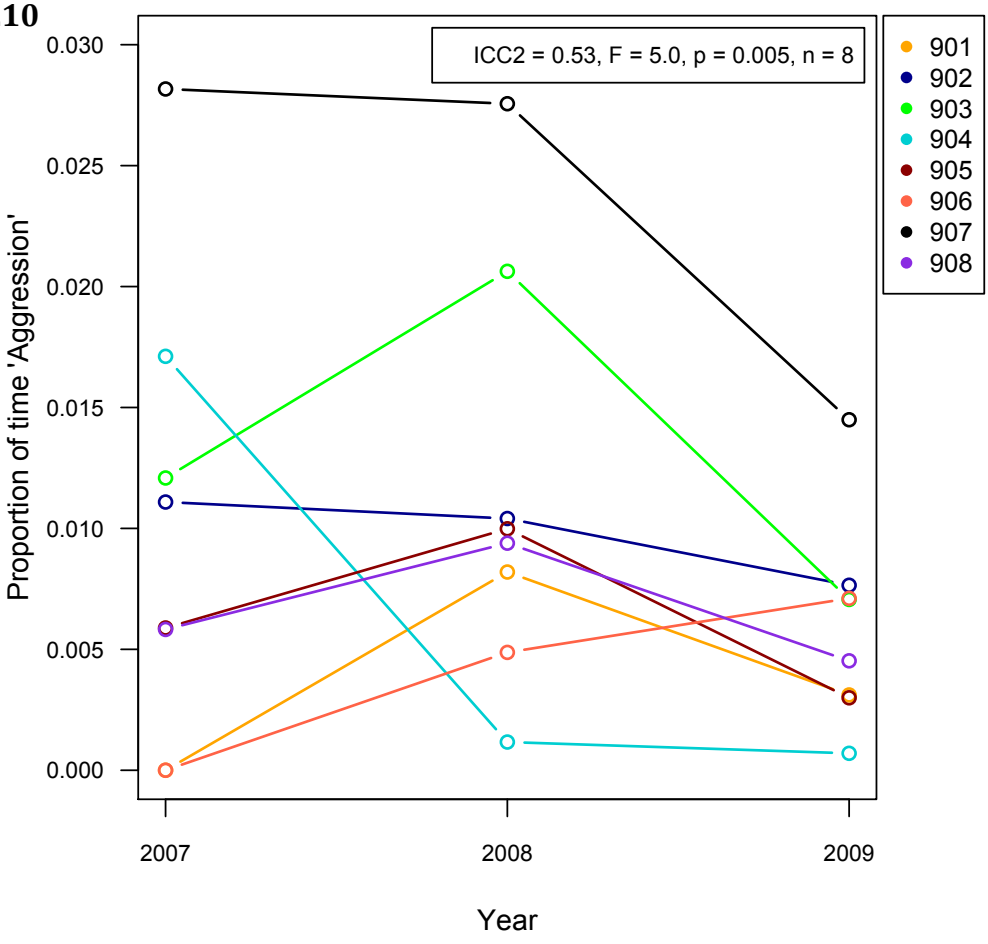
917
901
915
903
914
906
905
916
907
904
908

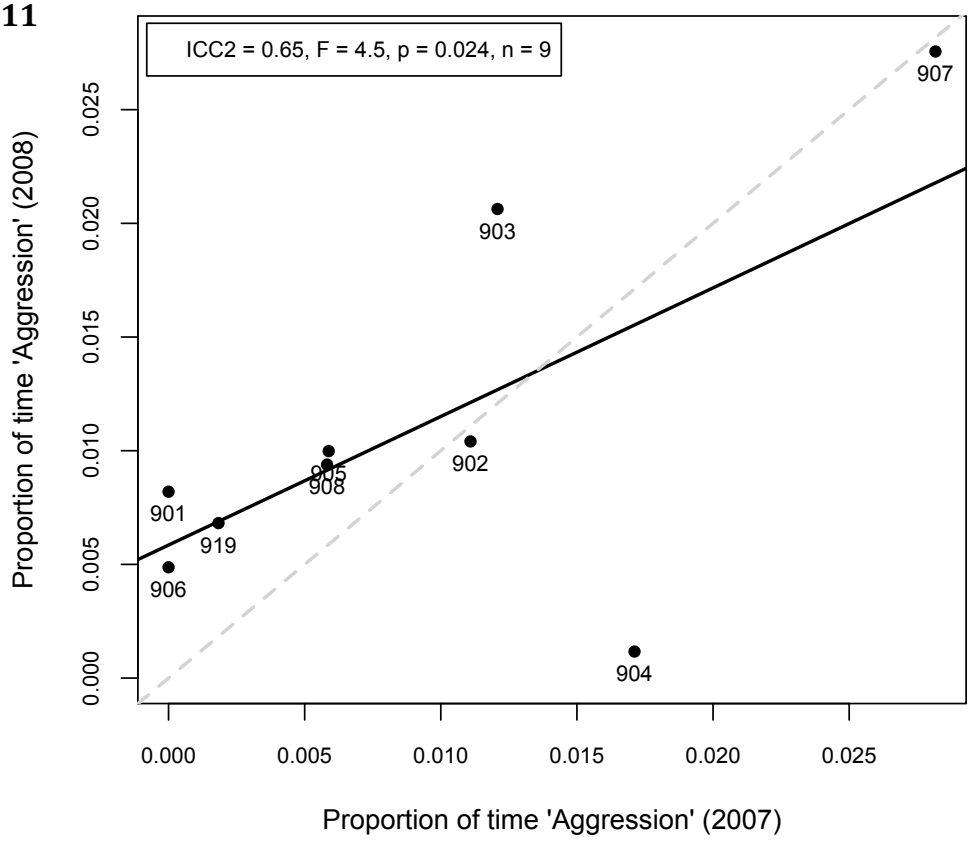
4.9


ICC2 = 0.55, F = 4.5, p = 0.024, n = 9
Proportion of time 'Pup Interactions' (2009)
Proportion of time 'Pup Interactions' (2007)
0.000
0.005
0.010
0.015
0.020
902
909
903
901
905
906
907
904
908

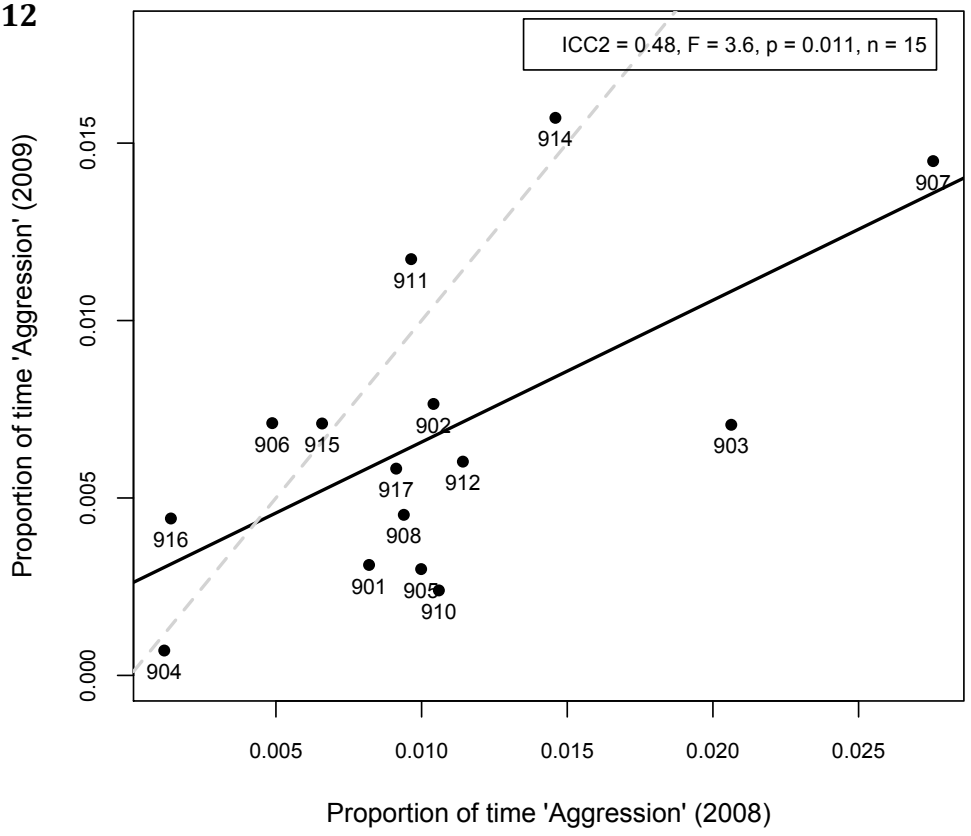
4.10


ICC2 = 0.53, F = 5.0, p = 0.005, n = 8
Proportion of time 'Aggression'
Year
2007
2008
2009
0.000
0.005
0.010
0.015
0.020
0.025
0.030
901
902
903
904
905
906
907
908

4.11


ICC2 = 0.65, F = 4.5, p = 0.024, n = 9
Proportion of time 'Aggression' (2008)
Proportion of time 'Aggression' (2007)
0.000
0.005
0.010
0.015
0.020
0.025
907
903
902
905
908
901
919
906
904

4.12


ICC2 = 0.48, F = 3.6, p = 0.011, n = 15
Proportion of time 'Aggression' (2009)
Proportion of time 'Aggression' (2008)
0.000
0.005
0.010
0.015
0.020
0.025
914
907
911
902
906
915
903
917
912
916
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901
905
910
904

4.6.2. The influence of site fidelity on CIDs in behaviour

The site fidelity of all re-sighted females was presented in Chapter 3, Section 3.10. Both the distance between pupping sites and the distance between the centre of the core area of the individuals' estimated home range showed considerable variation. The former ranged from 3.82 m to 66.52 m (median = 17.6 m), whilst the latter ranged from 1.3 m to 48.15 m (median = 17.87 m). As a visual example of how variable an individuals' home range usage was, the KDE isopleths for some of the individuals that were re-sighted in two or more breeding seasons are shown in Chapter 3 Figure 3.9.

Of the 24 pairwise ICC analyses, 9 were significantly repeatable (Table 4.2). The partial regression plots of the absolute residuals from the ICC analysis and both of the site fidelity measures are shown in Figures A4.1 - A4.9. The results of the Spearman's rank correlation coefficients are shown in the figure legends. Two of the 18 analyses were significant; these were the pup check ($r = 0.525$, $p = 0.047$, $n = 15$; Figure A4.1b) and alert ($r = -0.75$, $p = 0.025$, $n = 9$; Figure A4.4b) behavioural categories for the distance between the centre of the core area of the home range between the 2008 & 2009 and the 2007 & 2009 breeding seasons, respectively. The former was a positive relationship, whilst the latter was negative. It was expected that individuals that were closer to the same location in the previous breeding season would show less variability in their behaviour; therefore, the negative correlation between the site fidelity measure and alert is considered spurious. Conversely, the positive correlation between the site fidelity measure and the pup check behavioural category suggests that females that showed a higher degree of site fidelity (and were therefore presumably more familiar with their geographic location) also showed less variability in the proportion of time they spent pup checking.

4.7. Discussion

4.7.1. Comparable repeatability estimates

The repeatability estimates presented in this chapter are comparable to other studies. For example, Bell et al. (2009) carried out a meta-analysis on the repeatability of animal behaviour and, from a total of 759 estimates they calculated a mean repeatability estimate of 0.37 (Figure 4.13). They concluded that the data presented in their meta-analysis 'overwhelmingly support the hypothesis that behaviour is repeatable'. Strictly speaking, the repeatability estimates presented here should not be compared to the meta-analysis because Bell et al. (2009) were addressing the question: 'how repeatable is animal behaviour?' and did not consider the significance of the correlation coefficient. Since the focus of the current study was on behaviours that were significantly repeatable, these estimates would naturally give higher values. Nevertheless, the (significant and insignificant) repeatability estimates presented in the current study (Table 4.2) are comparable to the distribution of repeatability estimates presented by Bell et al. (2009; Figure 4.13). Consequently, the results presented in this chapter contribute to the growing number of studies that have shown that certain aspects of animal behaviour are repeatable.

4.7.2. Factors potentially influencing CIDs in behaviour

The repeatability estimate is the property of the group of individuals; therefore, the variation in the estimate will be influenced by which individuals are included in the group (Hayes & Jenkins, 1997; Bell et al., 2009). Furthermore, even if the ICC estimate is greater than zero it does not mean that all individuals within the group have behaved equally consistently, which explains why the individuals re-sighted in all three years did not maintain their rank order (despite the significant repeatability estimates for the alert, presenting & nursing and aggression behavioural categories). Therefore, some individuals' behaviour may be more (or less) consistent than others, which would have a considerable influence on the outcome of the analysis, particularly if the sample size of individuals is small.

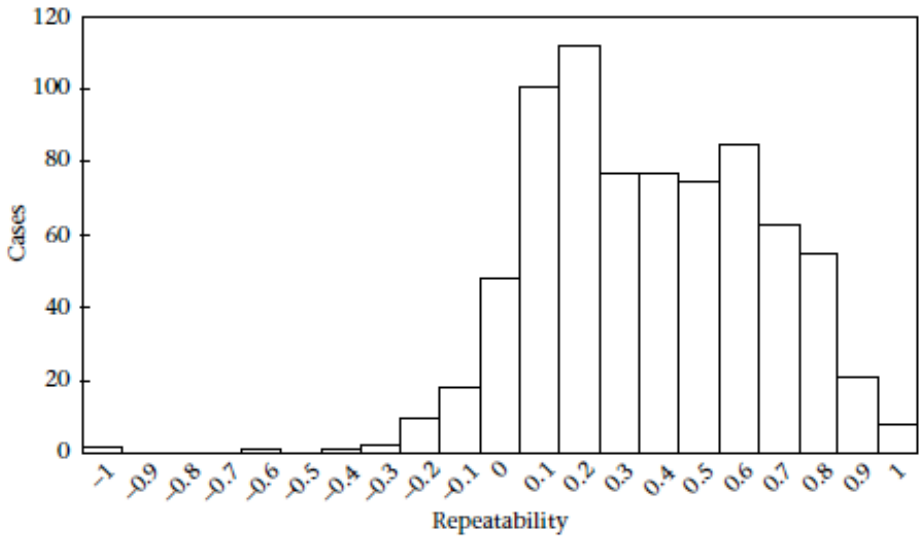


Figure 4.13: The distribution of 759 repeatability estimates from 114 studies, taken from Bell et al.'s (2009) meta-analysis on the repeatability of animal behaviour. All estimates that met the authors' criteria were included in the meta-analysis irrespective of the significance of the correlation coefficient.

There was evidence to suggest that the CIDs in the pup check behaviour may have been related to site fidelity, given that females that were closer to the centre of the core area of their home range were less variable in their time spent pup checking between breeding seasons. Although this was the only evidence that site fidelity may have influenced the repeatability of behaviour, it does seem likely that variation in behaviour would occur as a function of the intrinsic and/or extrinsic factors that each individual experienced, coupled with their behavioural responses to these stimuli (Bell & Aubin-Horth, 2010; Dingemanse et al., 2010; Dochtermann & Roff, 2010). Consequently, social (e.g. Webster et al., 2007; Cote et al., 2008; English et al., 2010; Krause et al., 2010), spatial (e.g. Verbeek et al., 1994; Clobert et al., 2009; Cote et al., 2010), environmental (e.g. Réale et al., 2003; Dingemanse et al., 2004; Minderman et al., 2009), and state-dependent (e.g. age, experience, condition) variables (e.g. Réale & Festa-Bianchet, 2003; Nussey et al., 2005a, b; Nussey et al., 2007b) may also influence the repeatability of behaviour. Some of these factors shall be addressed in the analyses presented in the subsequent chapters.

4.7.3. Previous studies on CIDs in the behaviour of wild grey seals

Previous studies by Twiss et al. (2011a) and Twiss & Franklin (2010) have shown that the pup check and the alert behaviours are highly repeatable in wild grey seals. Using in-field behavioural tests Twiss et al. (2011a) found that the pup check behaviour was highly repeatable *within* a breeding season (ICC2 = 0.80, $p \leq 0.001$, n = 20). Since they used a considerably different approach to the present study, it is not possible to directly compare these findings. Nevertheless, both have shown that the pup check behaviour is highly repeatable. However, in the present study, this behaviour was only repeatable in one of the four analyses, and there was evidence to suggest that this may have been influenced by site fidelity. In the second of these studies, Twiss & Franklin (2010) used the same sampling and analytical protocol as used in the present study to show that the alert behaviour of male grey seals was highly repeatable between two breeding seasons (ICC2 = 0.83, $p = 0.002$, n = 8). Furthermore, the individuals included in Twiss & Franklin's (2010) study were handled at the beginning and towards the end of their tenure on the breeding colony. Consequently, they were able to show that the repeatability of the alert behaviour was not related to several spatial or state-dependent variables. In the present study, the alert behavioural category was highly repeatable, highly robust and unrelated to site fidelity. Therefore, between Twiss & Franklin's (2010) study and the present study, there is substantial evidence, which suggests that, in adult grey seals during the breeding season, the alert behaviour is both highly, and robustly repeatable.

4.7.4. How does 'natural' behaviour relate to the behavioural axes

In observational studies of wild animals, it is important to consider how the behaviours examined relate to the 'classic' behavioural axes approach used in the laboratory and in in-field tests (e.g. Huntingford, 1976; Wilson et al., 1994; Réale et al., 2000; Réale et al., 2007). In the present study, the aggression behavioural category can be compared directly to the 'aggression behavioural axis' (Chapter 1, Section 1.3), which is defined as 'aggressive behaviour towards a conspecific'. More generally, the locomotion behavioural category could be likened to the 'activity behavioural axis', which is broadly defined as an individual's 'level of

activity'. Arguably, given this broad definition, other behavioural categories such as comfort movement and pup interactions could be included in this behavioural axis too. However, the behaviours observed during this study were deliberately separated into nine (including sex) behavioural categories because they were considered to be functionally different behaviours (Chapter 2, Section 2.5.3). Therefore, considering these behavioural categories collectively is not desirable, as this would limit the ability to biologically interpret the results of any subsequent analyses.

The 'shyness-boldness behavioural axis', which is defined as the 'reaction to a risky, but non-novel situation' could encompass the alert behaviour. For example, if a female performs an alert behaviour as a result of an approach by a conspecific, which she might perceive as a threat to her or her pup. However, alert individuals are not always responding to conspecifics (Culloch, pers. obs.); consequently, this behaviour may be more accurately described as an indication of an individual's 'awareness' and/or 'nervousness', rather than a measure of their boldness. The pup check behaviour may have similar attributes to alert, but it may be more specific to maternal care and/or an individual's mothering style. The functionality of these behaviours, and how they relate to the 'classic' behavioural axes shall be discussed in greater detail in Chapter 9, following the findings presented in the subsequent chapters.

4.7.5. The importance of robust repeatability estimates

How robust repeatability estimates were for each of the behavioural categories does infer something about the influence of the individuals that were included in the group and/or the variation in intrinsic and/or extrinsic factors between breeding seasons. For example, alert was the only behavioural category that was repeatable in all four analyses; therefore, which individuals were included in the group, and the variation in intrinsic and/or extrinsic factors between breeding seasons, had minimal influence on the repeatability of the alert behaviour. Conversely, the repeatability of other, less robustly repeatable behaviours, such as pup checking (which was only repeatable in one of the four analyses), was heavily influenced by which individuals were included in the group and/or the variation in

intrinsic and/or extrinsic factors between breeding seasons. For both of these behaviours the ICC2 and the ICC3 repeatability estimates were very similar (Tables 4.2 and A4.2); therefore, there was little systematic variation in these behaviours between breeding seasons. This suggests that the repeatability estimates were primarily influenced by the composition of individuals within the group, rather than the variation between extrinsic and/or intrinsic factors across breeding seasons. However, if the same individuals experience a similar environment across breeding seasons, as was found for the pup checking behaviour, then teasing apart the effect of the environment from the effect of the individual is both fundamentally important and extremely challenging (Dingemanse et al., 2010).

4.8. Conclusion

Certain aspects of the behaviour of wild postpartum grey seals were highly repeatable; however, there was considerable variation in the repeatability estimates between behavioural categories. Some were not repeatable at all (resting, comfort movement and locomotion), whilst others were robustly repeatable (alert). Although other studies have used observational techniques or 'hands-off' behavioural tests to address the repeatability of behaviour in wild animals (e.g. Twiss & Franklin, 2010; Twiss et al., 2011a), this is arguably the first study to use an entirely 'hands-off' observational approach to quantify whether or not the natural behaviour of wild animals whilst *in situ* are repeatable. Furthermore, the present study is also arguably the first to quantify whether or not certain behaviours are more robustly repeatable than others. However, to ascertain why repeatability in behaviour might occur, a second analytical approach is required, in order to identify which particular covariates best explain the variation in individual's behaviour.

Chapter Five:
Identifying whether or not individuals' identity is an important covariate for explaining variation in key behavioural categories

5.1. Introduction

The results presented in Chapter 4 showed that aspects of the behaviour of postpartum female grey seals whilst on the breeding colony were repeatable across breeding seasons. Furthermore, of the behaviours that were repeatable, there was considerable variation in how robust the repeatability estimates were. Consequently, whether or not the repeatability estimates for those particular behaviours were significant must have depended upon which individuals were included in the group and/or which breeding seasons were included in the analyses.

Of the estimates that were significantly repeatable, there was limited evidence to suggest that habitat selection and/or habitat usage was influencing the repeatability of behaviour, as determined by site fidelity measures. However, using site fidelity to address this question means that if females selected sites based on similar social and/or physical environments, then such sites may not necessarily be in the same geographical location. Therefore, females could have utilised similar resources and, as a consequence, behaved similarly across breeding seasons despite being in different geographic locations. Furthermore, the social and environmental variation that the groups of individuals experienced within and across breeding seasons was likely to be more complex than the site fidelity measure could account for. Therefore, at such a coarse temporal scale it is difficult to infer with confidence, whether or not consistent individual differences (CIDs) in behaviour can solely be attributed to the group of individuals and not the environment in which they were experiencing (Dingemanse et al., 2010). Previous studies have shown that environmental covariates, such as locations of pools, rainfall and air temperature do influence grey seal behaviour whilst on the breeding colony (Twiss et al., 2000; Redman et al., 2001; Twiss et al., 2002; Chapter 3, Section 3.14). However, no study has investigated whether or not any

of the variance in behaviour observed on grey seal breeding colonies can be explained by individuals' identity.

5.2. Aims

The principal aim of this chapter is to ascertain whether or not individual identity does, at least in part, explain variation in behaviour. In order to quantify this, the behavioural categories are modelled using social and environmental variables and individuals' identity as explanatory variables. Whether or not individual identity is retained within a model will be influenced (to a degree) by the composition of individuals within the group and the social and environmental variation that the individuals within the group experienced within and across breeding seasons. Therefore, to quantify the effects of these variables, and to ascertain how robust individual identity is with respect to a particular behaviour (i.e. how regularly it is retained within the models), each breeding season for each cohort of re-sighted individuals shall be modelled separately (i.e. there are a total of nine datasets: three for 2007 - 2009; two for 2007 & 2008; two for 2008 & 2009; two for 2007 & 2009). The results presented in this chapter shall be discussed in relation to the repeatability estimates presented in Chapter 4, with particular emphasis on whether or not individual identity is retained in the models that correspond to significant repeatability estimates.

5.3. Methods

In this chapter, the behavioural data were modelled using Generalised Linear Models (GLMs) with a beta-binomial distribution and a logit link (Crawley, 2007; Bolker, 2008; Zuur et al., 2009b). The beta-binomial distribution is preferred to a binomial distribution when the response variable exhibits too much spread (Bolker, 2008; Richards, 2008), which was the case for the majority of the datasets in the present study (Tables A5.1 and A5.2). Where this was not the case, using the binomial distribution as opposed to the beta-binomial distribution, would not have changed the inference made on any of the models (see Table A5.2). Therefore, to maintain consistency with respect to the analytical approach used for each of the behavioural categories and for each of the datasets, the beta-binomial

distribution was applied to all models. For more information on the beta-binomial distribution, see Section A of the Appendix.

5.3.1. Selecting the behavioural categories to be modelled

Based on previous studies and the results presented in Chapter 4, only the pup check, alert, aggression and locomotion behavioural categories were modelled in this chapter. The first three of these behaviours were selected because previous studies and/or the results presented in Chapter 4 have shown that these behaviours are repeatable in wild grey seals (Twiss & Franklin, 2010; Twiss et al., 2011a). However, with respect to the present study, the degree to which other factors are influencing repeatability needs to be addressed in greater detail. For example, Twiss & Franklin (2010) found that the repeatability of the alert behaviour in wild male grey seals was not influenced by covariates such as size, mass, age, length of stay on the colony, dominance or site fidelity. Conversely, the present study has only investigated the relationship between the repeatability of behaviour and site fidelity. Nevertheless, for the alert behavioural category, there was no evidence to suggest that site fidelity was influencing the repeatability of this behaviour. However, there was evidence to suggest that the repeatability of the pup checking behaviour was influenced by geographic location, and although no similar pattern was found for the aggression behavioural category, there is evidence to suggest that aggression influences the distribution and density of known individuals whilst on the breeding colony (Stephenson et al., 2007). Furthermore, there is also evidence that social associations between postpartum females do occur within some regions of the North Rona breeding colony (Pomeroy et al., 2005); therefore, the time spent in the aggression behavioural category may, in part, be influenced by an individual's familiarity with neighbouring seals. Consequently, this behaviour may be influenced by the physical and/or social environment, rather than site fidelity.

The locomotion behavioural category was selected because previous studies have shown, that whilst on the breeding colony, females have significantly greater rates of locomotion during extended dry periods (Redman et al., 2001). Furthermore, the analyses in Chapter 3, Section 3.14, showed that the distance

between a mother and her nearest pool was heavily influenced by environmental factors such as rainfall and air temperature. Therefore, unlike the pup check, alert and aggression behavioural categories, locomotion may be an example of a behaviour that is primarily determined by the environment, and not the individual. Consequently, it is expected that the social and/or environmental variables will explain all of the variation in locomotion. This hypothesis is supported by the results presented in Chapter 4, which found that the locomotion behavioural category was not repeatable in any of the four analyses.

5.3.2. The structure of the datasets

The data were analysed on an hourly basis, as explained in Chapter 3 Section 3.11. Each breeding season for each cohort of re-sighted individuals was modelled separately. All missing values (e.g. incidences where individuals had no spatial data for a given hour) were removed from each of the datasets in order to avoid model comparison between datasets of varying sizes (Grueber et al., 2011; Nakagawa & Freckleton, 2011). The response and the explanatory variables were not transformed, following growing support for fitting raw data directly to the proposed models (Bolker, 2008; Bolker et al., 2009; Richards et al., 2011; Warton & Hui, 2011; Chapter 3, Section 3.3). In Chapter 4, the lactation periods were used as a conservative approach to identify temporal variation in behaviour in the absence of potentially influential covariates (Chapter 3, Section 3.6). In the present chapter, the covariates that are suspected to influence this variation in behaviour during lactation are included in the models (Section 5.3.4); therefore, there is no need to use only the mid lactation period for the pup check or locomotion behavioural categories (Chapter 4, Section 4.5.1).

5.3.3. The relationship between the response and explanatory variables

As part of the exploratory analyses, the relationship between each of the four behavioural categories and the covariates of interest (which were introduced in Chapter 3, Section 3.8) was tested using a Spearman's rank correlation coefficient (Zuur et al., 2009a). This was done for each of the nine datasets, for the four behavioural categories and for all of the explanatory variables, irrespective of

whether or not they were omitted as a result of the collinearity analyses presented in Chapter 3, Section 3.14. In all analyses there was at least one significant relationship between a covariate and the response variable (Tables A5.3 - A5.6). However, the proportion of time a mother's pup spent active was the only covariate that was significant in all of the datasets for all four of the behavioural categories. In all instances, the relationship was positive; therefore, the more active the pup was, the more time the mother spent in each of the four behavioural categories.

5.3.4. The rationale for including each of the covariates

Based on the collinearity analyses presented in Chapter 3, Section 3.14, the covariates that were used in the following analyses are the:

1) Proportion of time the mother's pup spent active per hour,
2) Distance between the mother and her nearest female neighbour (m),
3) Distance between the mother and her nearest pool (m),
4) Mother's location within her estimated home range (using a Kernel Density Estimate),
5) Amount of rainfall (mm) per day,
6) Air temperature (^{o}C) as an average per hour,
7) Individuals' unique identification code (individuals' ID),

Covariates 2, 3 and 4 were taken at hourly intervals (for more information on covariates 2 - 6 see Chapter 2, Sections 2.5.6 - 2.5.7 and for more information on the first covariate see Chapter 3, Section 3.11). The decision to include these covariates in the following analyses was based on our current understanding of grey seal breeding ecology in the U.K., as detailed in published studies and from the data presented in this thesis (Chapter 3, Section 3.14). In addition, the sex of mothers' pups was of interest, as there is conflicting evidence as to whether or not differential maternal investment between the sexes occurs (Anderson & Fedak, 1987; Kovacs, 1987; Trillmich, 1996; Pomeroy et al., 1999). However, there were too few data to quantify this. Nevertheless, pup sex shall be included, were relevant, in the plots presented in the results, so that a qualitative assessment of

pup sex on behaviour can be made. Chapter 3, Section 3.14 directly discusses the importance of covariates 3, 4, 5 and 6; therefore, the justification for including these covariates shall not be reiterated here.

Of the other two continuous covariates: the activity of the pup was included because previous studies and the exploratory analyses presented in this chapter have shown that mothers do respond to their pup's behaviour (e.g. Fogden, 1971; Kovacs, 1987; Smiseth & Lorentsen, 2001; Tables A5.3 - A5.6); and the nearest female neighbour was included because postpartum female grey seals become intolerant of conspecifics that come within 2 body lengths (ca. 3 - 4 m; Boness et al., 1982; Caudron, 1998; Pomeroy et al., 2000b), which is comparable to the average distance between a female and her nearest female neighbour in the present study (ca. 5 m; Chapter 3, Section 3.8.1). Therefore, any activity on the colony is likely to result in a reaction from neighbouring individuals (Boness et al., 1982; Redman, 2002).

The primary aim of including individuals' ID in the analyses is to ascertain whether or not it is retained within a model, despite accounting for other potentially influential covariates. Consequently, if individuals' ID is retained, then this indicates that there is low within-individual variation and high between-individual variation in behaviour (Hayes & Jenkins, 1997; Bell et al., 2009; Chapter 4, Section 4.2). It is important to note that the analytical approach used in this chapter is not attempting to quantify whether or not the individual variation was consistent between breeding seasons. Rather, it intends to identify which covariates (including individuals' ID) best explain the variation in behaviour.

5.3.5. The rationale for the modelling approach used

In this chapter, model selection and model inference shall be made using the second order Aikake's Information Criterion (AICc; Burnham & Anderson, 2002). AICc is preferred over Aikake's Information Criterion (AIC) when the ratio between sample size (*n*) and the number of parameters (*K*) is small. Although this is unlikely to be an issue in the present study, it is still recommended that AICc is used as a conservative default, because as the sample size increases in relation

to the number of parameters, the difference between AIC and AICc becomes negligible (Burnham & Anderson, 2002; Burnham et al., 2011; Grueber et al., 2011). The methodologies described in this and subsequent chapters do assume prior knowledge of AICc (and AIC); however, for those not familiar with these information theoretic (IT) approaches, see Section B of the Appendix for a short review. The review includes a more detailed description of the approaches used for model selection and model inference, and also provides information and discussion on alternative approaches that were not used in this thesis. Both AIC and AICc are used in the same manner in model selection and model inference; consequently, the term AICc will be used throughout, but it should be considered synonymous with AIC unless otherwise stated.

5.3.6. The approach for model selection

A global model (a model that contains all of the covariates of interest) for each of the behavioural categories was constructed, and every potential model within the global model was tested and ranked by its $\triangle$ value. No interaction terms were included in the models presented in this chapter because the inclusion of interactions within a (global) model often results in overly complex models being retained within the confidence set. Furthermore, where interaction terms are retained, the model output can be very difficult to biologically interpret (Schielzeth, 2010; Garamszegi, 2011; Mundry, 2011; see Section B of the Appendix for more details). With the exception of Individual ID, which was included as a categorical variable, all of the other covariates were included as continuous variables. By including individual ID as a categorical variable, every individual included in the model is regarded as an additional parameter, and thus increases the ratio of n/K (See Eq. 1 in Section B of the Appendix). It is acknowledged that an alternative approach to analysing these data would be to include individual as a random-effect within a Generalised Linear Mixed Model (GLMM; Bolker, 2008; Bolker et al., 2009; Zuur, et al., 2009b). However, there are a number of caveats that need to be taken into account when using this approach, which shall be discussed in the subsequent chapter. Nevertheless, the approach of fitting a fixed-effect GLM is a recommended step, prior to carrying out a GLMM (Gelman & Hill, 2006; Pinheiro & Chao, 2006; Bolker, 2008; Bolker, et al., 2009).

Based on Richards (2008) and Richards et al.'s (2011) rules of thumb, the present study used five steps to select the models retained within the confidence set. For the first step, models within $\triangle < 6$ of the 'best' model (the model with the lowest AICc) were retained within a preliminary confidence set. For the second step, all simpler models within the preliminary confidence set that were nested within more complex models (where both models contain the same terms but the more complex model had at least one additional term and a higher $\triangle$ value) were omitted from the preliminary confidence set. The third step assessed whether or not collinearity occurred in any of the models retained within the preliminary confidence set (which was checked using the relevant tables; Chapter 3, Appendix, A3.4 - A3.12). If collinearity did occur, then all combinations of the non-collinear covariates were considered. To assess whether or not collinearity of the continuous covariates influenced the effect of individuals' ID, the individuals' ID was included and excluded from all the resulting model combinations. For example, if covariates *x* and *y* were retained in a model but both were collinear, then four separate models would be considered (i.e. model 1 (*x*), model 2 (*y*), model 3 (*x* + individuals' ID) and model 4 (*y* + individuals' ID)). After this step, steps one ($\triangle < 6$) and two (model nesting) were repeated on the resulting group of models. Consequently, these five steps for model selection resulted in the confidence set of models that was used in the subsequent multi-model inference. If individuals' ID was not retained within the confidence set then the 'best' model that retained this covariate was also presented, for comparison purposes only.

5.3.7. The approach for model inference

The influence of individuals' ID on behaviour was of particular interest; therefore, inference was made on the simplest model that retained this covariate. If individuals' ID was not retained in any of the models within the confidence set, then inference was made on the simplest model (Richards et al., 2011). For continuity, the term 'simplest model' shall be used throughout to refer to models that include individuals' ID, although it is acknowledged that the inclusion of individuals' ID may mean that the model is not the simplest model retained within the confidence set. Continuous covariates retained within a model were considered influential if they had an estimate that was more than twice the

standard error of the estimate (Crawley, 2007). If individuals' ID was retained in a model then this will be indicated in the model tables, but the effect size for each individual shall not be presented as these are relative to the individual that is retained within the intercept of the model (Crawley, 2007). Although it was desirable to identify which social and/or environmental covariates best predicted the behaviour, the principal aim of these analyses was to identify whether or not social and/or environmental covariates fully explained behaviour. Therefore, the conservative approach (described in Section 5.3.6) to dealing with multi-collinearity amongst covariates may have resulted in the 'true' influential covariate being omitted from the confidence set. However, when making inference on the models retained within the confidence set, the collinearity of the covariates shall be taken in to consideration.

5.3.8. Goodness-of-fit and model criticism

Testing the goodness-of-fit of a model is often done using the Pearson chi-square statistic ((expected-observed)^2 / expected), which tests whether the variance around the model predictions is greater than expected (Crawley, 2007; Zuur et al., 2009b). However, this test will only work for simple count data where the answers fall into discrete groups. If the data are continuous, or if an overdispersed distribution is used (such as the negative binomial, beta-binomial or zero-inflated binomial), then the model contains a parameter describing the variance and the chi-squared test is no longer useful (Bolker, 2008). Under these circumstances it is common practice to divide the data into discrete subsets so that the predicted and observed distributions can be compared (Chen et al., 2006; Bolker, 2008; Chen et al., 2008). In the present study, the predicted values were extracted from the simplest model and were plotted against the observed values. These plots were used as the initial stage in assessing the goodness-of-fit of the model (Bolker, 2008).

In the present study, the response variable will produce discrete values (for example, if the number of scan samples = 12 then there are only 13 (including 0) potential values that the response variable can take), whereas the predicted values are continuous (ranging between 0 and 1; Bolker, 2008 and Appendix,

Section A). Consequently, to assess the goodness-of-fit, only data obtained from the same number of scan samples (n) can be used. Given that n = 12 occurred more than any other sample size (ca. 70% of the data across the three years; Chapter 3, Table 3.11) these data were used for 2008 and 2009. In 2007, because of the different sampling regime (Chapter 2, Section 2.5.4) n = 6 occurred more than any other sample size. Consequently, goodness-of-fit was only assessed using these data (n = 6, 2007; n = 12, 2008 and 2009), which are assumed to be a representative sample of the entire dataset. In order to plot the goodness-of-fit, the predicted values were rescaled to equate to the number of times in which the behaviour was observed in an hour (or 30 minutes in 2007). The predicted and the observed data were binned, such that the bins were comprised of the observed values that ranged between 0 - 0.9˙, 1 - 1.9˙, 2 - 2.9˙, and so on (until n = 6 for 2007 and n = 12 for 2008 and 2009). The fitted and observed data were plotted alongside one another and the goodness-of-fit was visually assessed.

Using the simplest model, the response variable was predicted for covariates that had an estimate greater than twice the standard error. In order to do this, the covariate of interest was allowed to vary within its observed range whilst the other covariates retained within the simplest model were standardised to their mean (Crawley, 2007). For the observed values, the continuous covariates were binned at standard intervals; for example, for the proportion of time the pup spent active the data were binned at 0.1 intervals. In this instance, the extreme values (0 and 1) were given discrete bins because they were not uncommon occurrences (and inevitable values if only one scan sample was collected in a given hour; Chapter 3, Section 3.11). Therefore, in this example, the bins were divided such that the first bin = 0; the second bin = > 0 - 0.1; the third bin = > 0.1 - 0.2; and so on, up until the final bin, which = 1. Therefore, where the pup activity was 'standardised to its mean', the average time spent in behaviour *x* was calculated for each of the eleven bins. Where individuals' behaviour was standardised to its mean, the average time spent in behaviour *x* was calculated for the group of re-sighted individuals'.

The predict() function in R was used to obtain the fitted values from the simplest model. To obtain the 95% confidence intervals, the observed and fitted

data were bootstrapped following the methodology presented in Chapter 3, Section 3.7. The models presented in this chapter were carried out in R using the function betabin() in the package *aod* (Lesnoff & Lancelot, 2011).

5.4. Results

The number of models retained at each of the five stages of the model selection process is shown in Table A5.7. Collinearity between covariates occurred in 20 of the 30 confidence sets. For each of the datasets the number of models retained from a possible 127 ranged between 1 and 5 (median = 2). For the 2007 datasets it was not possible to include individuals' ID in the models for the aggression or the locomotion behavioural categories because there were too few occurrences of these behaviours for some individuals. This is likely to be a product of the sampling protocol used in 2007 (Chapter 2, Section 2.5.4) coupled with the fact that these behaviours were infrequently recorded (Chapter 3, Section 3.4). Therefore, the aggression and locomotion models for the 2007 datasets are not presented. Only the $\triangle$ values are presented in the model tables, as the AICc values themselves are uninformative (Bolker, 2008).

5.4.1. Model output

The following sections shall present the results for each of the four behavioural categories. The term 'fitted values' shall refer to the values extracted from the model and the term 'predicted values' shall refer to those values predicted by the model whilst other covariates were standardised to their mean. The 95% confidence intervals for the observed values are represented by error bars, whilst the 95% confidence intervals for the fitted values are represented by either error bars or a dashed black line. All of the models that were retained within the confidence sets for the four behavioural categories shall be presented in the model tables. To avoid presenting multiple plots, inference shall be made for each year using the 2007 models for the individuals re-sighted in 2007 & 2008, and the 2008 and 2009 models for the individuals re-sighted in 2008 & 2009. The model-checking plots for these models best illustrated the general trends found throughout the data and maximise the sample sizes (number of scan samples and

number of re-sighted individuals). The collinearity of covariates shall be considered in the discussion.

5.4.2. Pup check models

There were eighteen models retained across the nine confidence sets for the pup check behavioural category (Table 5.1). Of these eighteen models, individuals' ID was retained in half of them (9/18). The activity of the pup was retained in all of the models (18/18), and there was also support for the distance to the nearest pool (6/18), the distance to the nearest female neighbour (1/18) and the amount of rainfall (2/18). With the exception of the activity of the pup, the only other covariate that was retained in the three confidence sets for the same breeding season was the distance to the nearest pool in 2009. However, the estimates for the distance to the nearest pool, the distance to the nearest female neighbour and rainfall were typically close to, or less than, twice the standard error (Table 5.1). Therefore, the simplest model for all of the datasets included pup activity, only. However, because individuals' ID was retained in some of the models within the confidence sets, the model retaining pup activity and individuals' ID shall be used for inference.

The overdispersion coefficient for the pup check models always had an estimate that was less than twice the standard error for all the models. Therefore, the additional binomial error provided by the beta-binomial distribution was not required (Appendix, Section A). Nevertheless, the goodness-of-fit plots show that the observed frequency of the pup check behavioural category fitted the beta-binomial distribution well (Figure A5.1). The between- and within-individual variation in the pup checking behaviour was evident from the plots of the observed data (Figure 5.1). The model fitted these data well, although the within-individual variation was typically less for the fitted values, which is particularly evident for individuals with small sample sizes. Where the activity of the pup was standardised to its mean, the accuracy of the predictions in relation to the mean observed and mean fitted values deviated more for some individuals than others.

Table 5.1: The summary for each of the models that were retained within the confidence set for individuals that were re-sighted in all three years (2007 - 2009; n = 8), 2007 & 2008 (n = 9), 2008 & 2009 (n = 15) and 2007 & 2009 (n = 9) for the **pup check behavioural category** (the number of models that were retained at each of the 5 stages of the model selection process is shown in Table A5.7). The models are arranged using the △ value; the AICc value is not presented. With the exception of ID, if the covariate was retained within the model then the estimated effect (Est.) and the standard error of the estimate (SE) are included in the table. ID is a categorical covariate; it was only of interest to know whether it was retained (✓) or not (X). Where ID was not retained within the confidence set the 'best' model containing this covariate is presented in bold italics in the last row of each of the confidence sets, irrespective of its △ value. See the footnote for definitions of the covariates and of abbreviations. The covariates HOME and TEMP were not retained in any of the models within the nine confidence sets, and were therefore omitted from the table. Table 5.1 is continued overleaf.

						Covariates										
		Intercept		**ODC**		**ACT**		**NFN**		**POOL**		**RAIN**		**ID**		
Analyses	**Year**	**Est.**	**SE**	**Est.**	**SE**	**Est.**	**SE**	**Est.**	**SE**	**Est.**	**SE**	**Est.**	**SE**		**d.f.**	**△**
2007 – 2009	2007	-5.422	0.641	0.004	0.012	1.290	0.129	-	-	-	-	-	-	✓	10	0
	2008	-4.709	0.162	0.005	0.005	1.266	0.259	-	-	0.026	0.015	-	-	X	4	0
		-4.588	0.144	0.005	0.006	1.273	0.259	-	-	-	-	-	-	X	3	0.958
		-5.359	***0.475***	***0.003***	***0.005***	***1.360***	***0.270***	***-***	***-***	***0.053***	***0.026***	***-***	***-***	✓	***11***	***6.599***
	2009	-4.965	0.178	0.002	<0.001	1.398	0.273	-	-	0.037	0.012	-	-	X	4	0
		-4.972	***0.290***	***<0.001***	***<0.001***	***1.473***	***0.280***	***0.046***	***0.021***	***0.033***	***0.018***	***-***	***-***	✓	***12***	***5.669***
2007 & 2008	2007	-5.356	0.631	0.004	0.011	1.402	0.364	-	-	-0.135	0.095	-	-	✓	12	0

		-5.470	0.643	0.003	0.012	1.395	0.361	-	-	-	-	-	-	✓	11	0
	2008	-4.711	0.155	0.006	0.005	1.282	0.248	-	-	0.025	0.015	-	-	X	4	0
		-4.603	0.139	0.006	0.005	1.290	0.248	-	-	-	-	-	-	X	3	0.737
		-5.435	***0.496***	***0.005***	***0.005***	***1.368***	***0.260***	***-***	***-***	***0.047***	***0.026***	***-***	***-***	✓	***12***	***9.096***
2008 & 2009	2008	-5.270	0.474	0.006	0.004	1.661	0.184	-	-	-	-	-0.016	0.012	✓	18	0
		-5.337	0.474	0.008	0.004	1.628	0.185	-	-	-	-	-	-	✓	17	0.840
	2009	-4.772	0.277	0.008	0.005	1.348	0.185	-	-	0.022	0.013	-	-	✓	18	0
		-4.835	0.283	0.008	0.005	1.376	0.185	-	-	-	-	0.014	0.009	✓	18	0.541
		-4.832	0.285	0.008	0.005	1.413	0.185	-	-	-	-	-	-	✓	17	0.943
2007 & 2009	2007	-5.412	0.610	<0.001	<0.001	1.195	0.347	-	-	-	-	-	-	✓	11	0
		-4.106	0.162	0.002	<0.001	1.298	0.343	-	-	-	-	-	-	X	3	4.632
	2009	-5.001	0.172	0.002	<0.001	1.483	0.263	-	-	0.030	0.012	-	-	X	4	0
		-5.078	0.204	0.002	0.004	1.558	0.265	0.032	0.018	-	-	-	-	X	4	2.968
		-4.863	0.163	0.003	0.005	1.587	0.264	-	-	-	-	-	-	X	3	4.063
		-5.092	***0.296***	***<0.001***	***<0.001***	***1.619***	***0.270***	***0.052***	***0.019***	***-***	***-***	***-***	***-***	✓	***12***	***3.587***

ACT: proportion of time the pup spent active; **NFN**: the distance between a mother and her nearest female neighbour (m); **POOL**: the distance between a mother and her nearest pool (m); **HOME**: the location of the female within her estimated home range (Kernel Density Estimate), which ranges from 1 - 100, where 100 is the centre of the core area of the home range; **RAIN**: the volume of rain that fell from the end of observations on day *x* and the end of observations on day *x*+1 (mm); **TEMP**: air temperature (^{o}C); **ID**: Individuals' identification code. With the exception of rainfall the other spatial and environmental covariates were recorded at hourly intervals; **ODC**: overdispersion coefficient; **d.f.**: degrees of freedom.

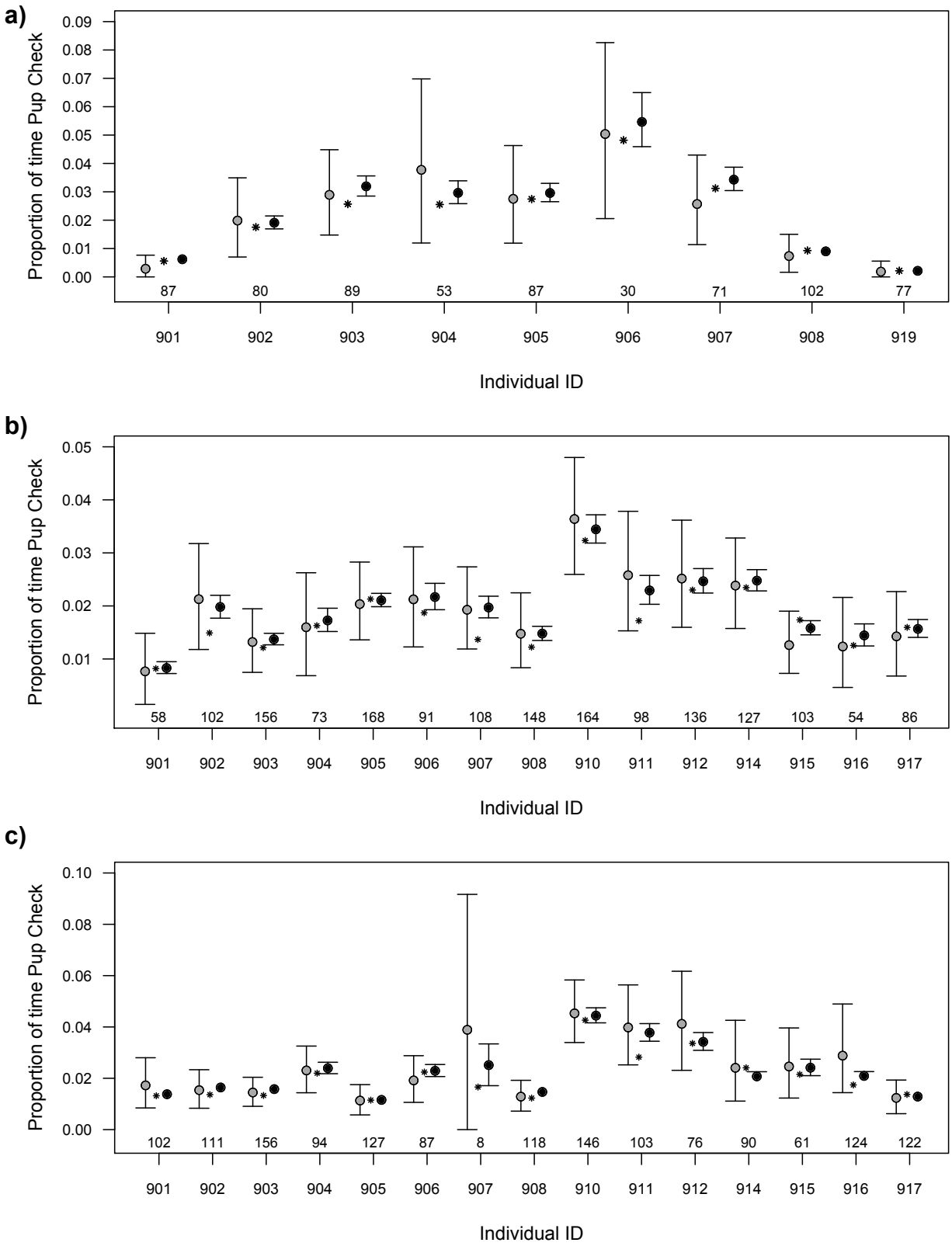


Figure 5.1: The mean observed (grey) and the mean fitted (black) proportion of time that each of the re-sighted individuals spent pup checking in the **a)** 2007 (2007 & 2008 re-sighted individuals) **b)** 2008 and **c)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons; * indicates the predicted value for each individual whilst the other covariates were standardised to their mean. The total number of hours that each individual was observed is noted on the inside of the x-axis. The covariates retained in each of these models are noted in Section 5.4.2.

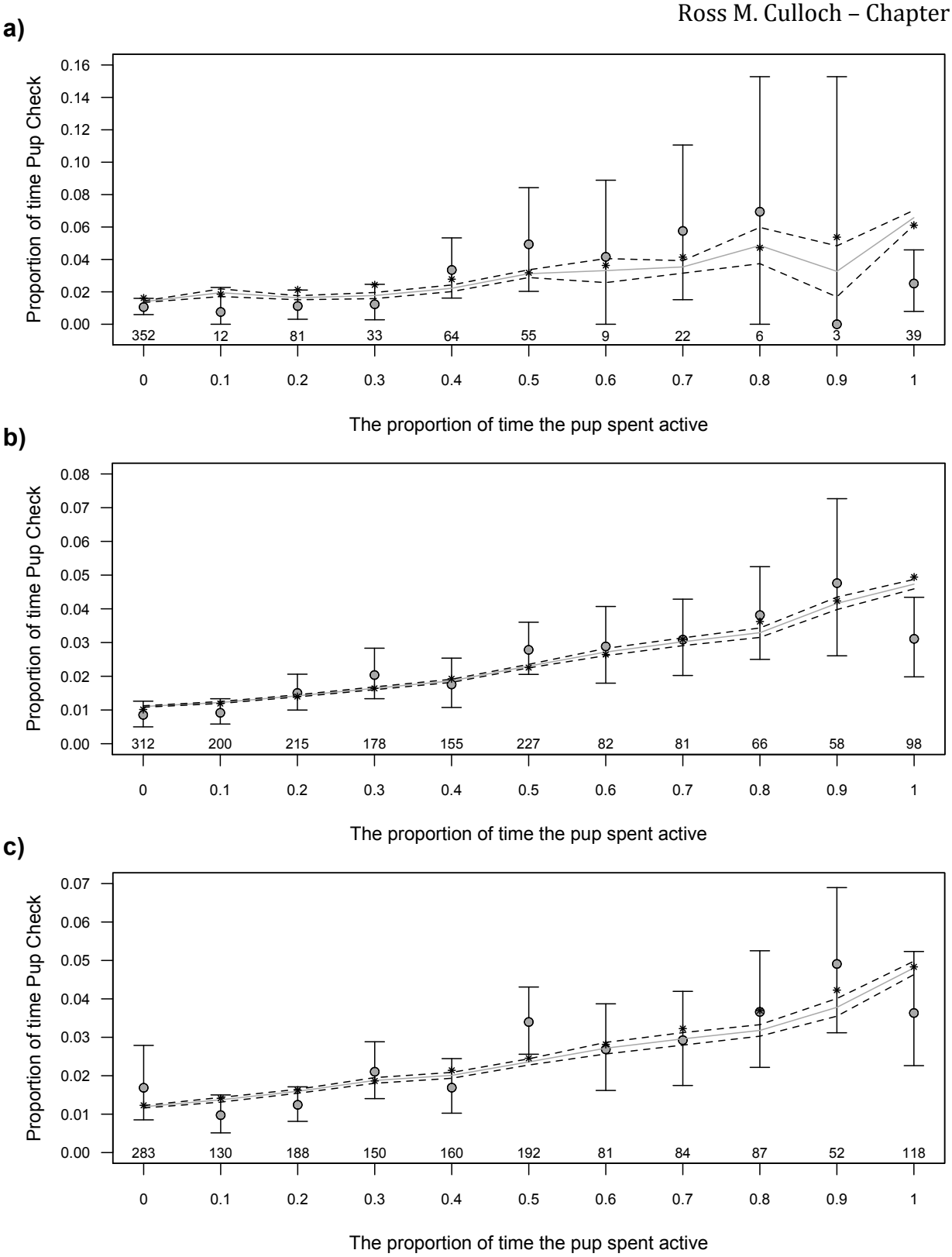


Figure 5.2: The mean observed (grey dots) and the mean fitted (grey line) proportion of time females spent pup checking in the **a)** 2007 (2007 & 2008 re-sighted individuals) **b)** 2008 and **c)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons across the observed range of pup activity; * indicates the predicted value for each bin of data whilst the other covariates were standardised to their mean. The value on the inside of the x-axis shows the number of data points (hourly scan samples) within the respective bin. The covariates retained in each of these models are noted in Section 5.4.2.

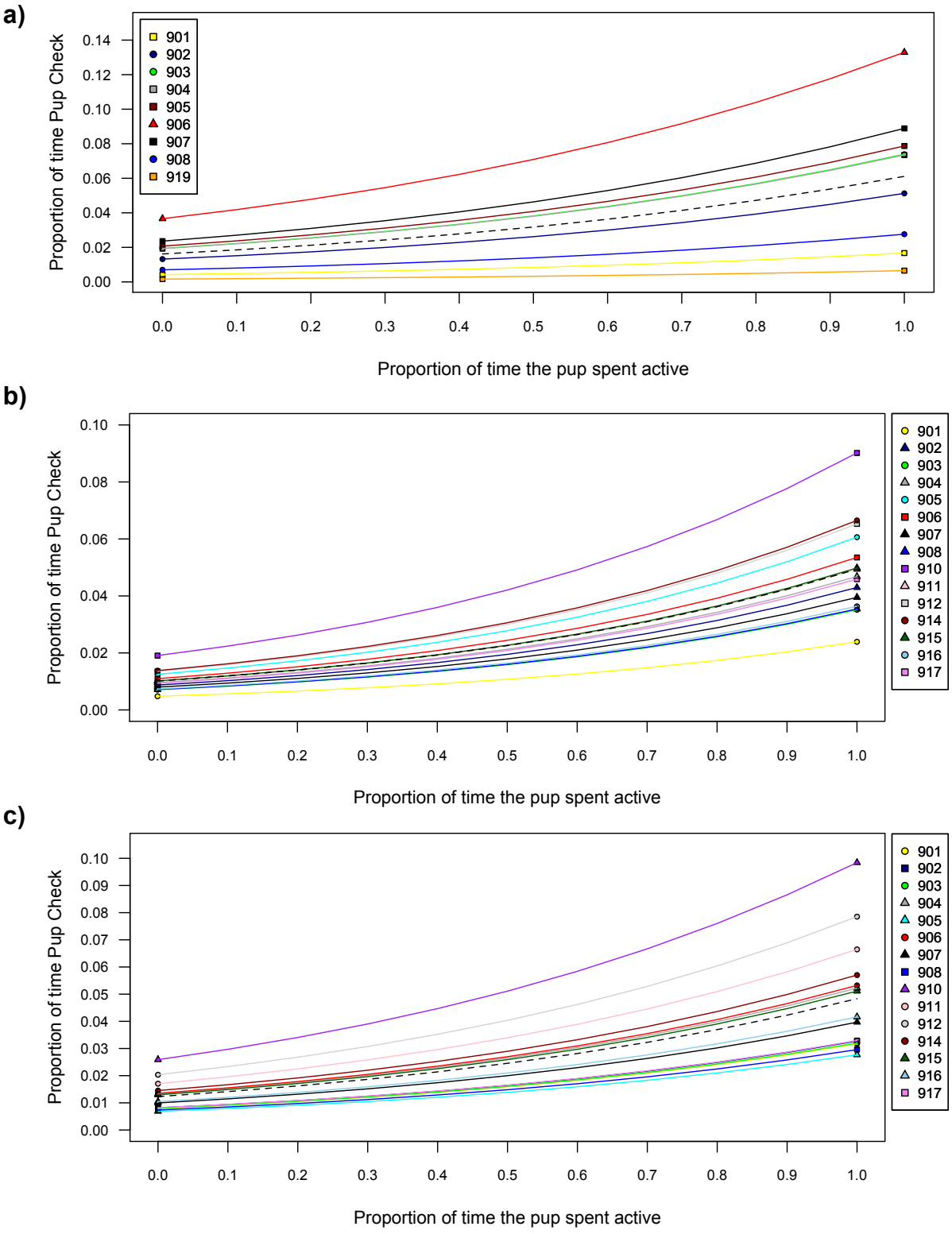


Figure 5.3: The predicted values for the proportion of time each individual spent pup checking in the **a)** 2007 (2007 & 2008 re-sighted individuals) **b)** 2008 and **c)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons across the observed range of pup activity. The mean of the group is shown as the black dashed line. Each individual has a unique colour code, which is shown in the legend, and is maintained throughout the plots presented in this chapter. The squares, circles and triangles indicate that the sex of the pup was female, male or unknown, respectively.

The models showed that as the pup becomes more active, the mother spends more time pup checking (Table 5.1; Figure 5.2). Notably, this pattern was less pronounced and more variable for the 2007 datasets, where there were fewer data available (Figure 5.2a). For the most part, the models predicted these data well; however, the models did tend to overestimate the proportion of time the mother spent pup checking when the pup was at its most active (Figure 5.2). Where the average time spent pup checking was calculated for the group of re-sighted individuals' (i.e. where individuals' ID was 'standardised to its mean'), the predicted values were similar to the mean fitted and mean observed values. This was particularly true for the mean fitted values at higher proportions of pup activity (Figure 5.2).

The plots for the predicted proportion of time spent pup checking for each individual across the observed range of pup activity reiterates that individual variation in this behaviour does occur, and that the activity of the pup is considerably influential (Figure 5.3). These figures also reiterate that the relationship between the pup checking behaviour and the activity of the pup is less pronounced for the 2007 datasets (Table 5.1; Figure 5.3a). In all three plots there are individuals that substantially increase the between-individual variation of the group. For example, individual 906 in 2007, individual 910 in 2008 and 2009 and individual 903 in 2009 all spend a comparably higher proportion of time pup checking (Figures 5.1 and 5.3). Although data are limited, there is no obvious pattern across the years to suggest that the sex of the pup is influencing a mother's pup checking behaviour.

5.4.3. Alert models

There were twenty-three models retained across the nine confidence sets for the alert behavioural category (Table 5.2). Individuals' ID was retained in all models (23/23), the activity of the pup was retained in the majority (20/23), and there was also varied but limited support for the distance to the nearest female neighbour (4/23), the distance to the nearest pool (5/23), home range usage (1/23) and rainfall (4/23). With the exception of the individuals' ID, the only other covariate that was retained in the three confidence sets for the three breeding

seasons was the activity of the pup. The distance to the nearest pool was retained in the 'best' model for the three confidence sets for the 2007 breeding season, and the distance to the nearest female neighbour and rainfall were retained in the three confidence sets for the 2008 breeding season. However, with the exception of the activity of the pup, the estimates for all of the continuous covariates were typically close to, or less than, twice the standard error (Table 5.2). Therefore, the simplest model for all datasets for the alert behavioural category included individuals' ID and pup activity.

The estimate for the overdispersion coefficient was more than twice the standard error for all models, which indicates that the additional binomial variation did improve the model (Table 5.2). This is supported by the goodness-of-fit plots, which show that the observed frequency of the alert behaviour fitted the beta-binomial distribution well (Figures A5.2). The between- and within-individual variation in the alert behaviour is evident from the plots of the observed data (Figure 5.4). The model fitted these data well, although similar to the pup checking behaviour, the within-individual variation was typically less for the fitted values, which is particularly evident for individuals with small sample sizes. Where the activity of the pup was standardised to its mean, the accuracy of the predictions in relation to the mean observed and mean fitted values deviated more for some individuals than others.

The models showed that the more active the pup was, the more alert the mother was (Table 5.2). The models for the 2008 and 2009 breeding seasons predicted these data well across the entire range of pup activity (Figure 5.5b,c). However, this pattern was considerably less pronounced and more variable for both the observed and fitted data for the 2007 breeding season, where there were fewer data available (Figure 5.5a). The predicted values were similar to the fitted and observed values for the 2008 and 2009 models, although in the latter breeding season, they tended to overestimate the proportion of time spent alert at higher proportions of pup activity (Figure 5.5b,c). For the 2007 breeding season, despite greater variability in the data at higher proportions of pup activity, the predicted values were similar to the fitted values, particularly at higher proportions of pup activity (Figure 5.5a).

Table 5.2: The summary for each of the models that were retained within the confidence set for individuals that were re-sighted in all three years (2007 - 2009; n = 8), 2007 & 2008 (n = 9), 2008 & 2009 (n = 15) and 2007 & 2009 (n = 9) for the **alert behavioural category** (the number of models that were retained at each of the 5 stages of the model selection process is shown in Table A5.7). The covariate TEMP was not retained in any of the models within the nine confidence sets, and was therefore omitted from the table. See Table 5.1 for the complete table legend, and see the footnote for Table 5.1 for definitions of the covariates and of abbreviations. Table 5.2 is continued overleaf.

						Covariates												
		Intercept		ODC		ACT		NFN		POOL		HOME		RAIN				
Analyse	Year	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	ID	d.f.	△
2007 –	2007	-3.568	0.292	0.055	0.018	0.854	0.284	-	-	0.134	0.072	-	-	-	-	✓	11	0
2009		-3.503	0.292	0.058	0.018	0.860	0.286	-	-	-	-	-	-	-	-	✓	10	1.803
	2008	-3.589	0.268	0.038	0.007	1.151	0.156	-	-	-	-	-	-	-0.021	0.01	✓	11	0
		-3.882	0.292	0.038	0.007	1.178	0.156	0.028	0.017	-	-	-	-	-	-	✓	11	2.125
		-3.682	0.264	0.038	0.007	1.170	0.156	-	-	-	-	-	-	-	-	✓	10	2.458
	2009	-3.524	0.177	0.024	0.007	1.231	0.167	-	-	-	-	-	-	-	-	✓	10	0
2007 &	2007	-3.518	0.284	0.05	0.017	0.799	0.279	-	-	0.145	0.070	-	-	-	-	✓	12	0
2008		-3.470	0.287	0.053	0.017	0.81	0.280	-	-	-	-	-	-	-	-	✓	11	2.147
		-3.320	0.274	0.052	0.017	-	-	-	-	0.141	0.070	-	-	-	-	✓	11	5.658
	2008	-3.638	0.276	0.04	0.007	1.135	0.155	-	-	-	-	-	-	-0.021	0.01	✓	12	0
		-3.966	0.300	0.04	0.007	1.167	0.155	0.031	0.017	-	-	-	-	-	-	✓	12	1.688
		-3.7	0.267	0.04	0.007	1.163	0.155	-	-	-	-	-	-	-	-	✓	11	2.672

2008 &	2008	-3.974	0.277	0.038	0.005	1.273	0.111	0.034	0.013	-	-	-	-	-	-	✓	18	0
2009		-3.691	0.266	0.038	0.005	1.264	0.111	-	-	-	-	-	-	-0.012	0.007	✓	18	1.780
		-3.742	0.263	0.039	0.006	1.284	0.112	-	-	-	-	-	-	-	-	✓	17	2.026
	2009	-3.542	0.176	0.039	0.006	1.193	0.118	-	-	-	-	-	-	0.01	0.006	✓	18	0
		-3.528	0.176	0.039	0.006	1.184	0.118	-	-	-	-	-	-	-	-	✓	17	1.066
2007 &	2007	-3.470	0.286	0.058	0.017	0.709	0.276	-	-	0.110	0.070	-	-	-	-	✓	12	0
2009		-3.239	0.504	0.061	0.018	0.700	0.278	-	-	-	-	-0.003	0.005	-	-	✓	12	2.398
		-3.467	0.330	0.062	0.018	0.733	0.277	-0.012	0.042	-	-	-	-	-	-	✓	12	2.709
		-3.338	0.282	0.061	0.018	-	-	-	-	0.110	0.070	-	-	-	-	✓	11	4.204
		-3.265	0.278	0.063	0.018	-	-	-	-	-	-	-	-	-	-	✓	10	4.657
	2009	-3.562	0.179	0.027	0.007	1.226	0.161	-	-	-	-	-	-	-	-	✓	11	0

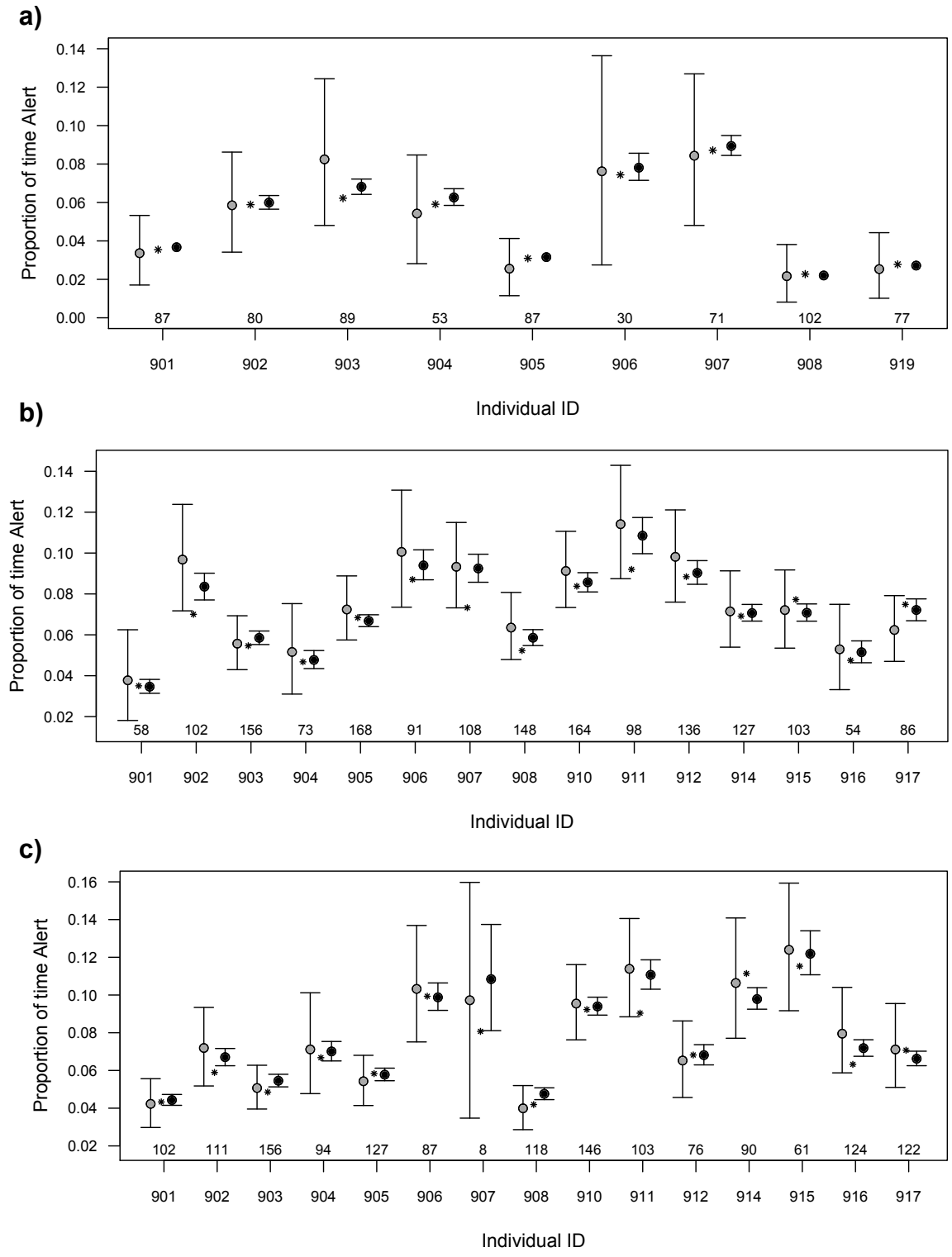


Figure 5.4: The mean observed (grey) and the mean fitted (black) proportion of time that each of the re-sighted individuals spent alert in the **a)** 2007 (2007 & 2008 re-sighted individuals) **b)** 2008 and **c)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons; * indicates the predicted value for each individual whilst the other covariates were standardised to their mean. The total number of hours that each individual was observed is noted on the inside of the x-axis. The covariates retained in each of these models are noted in Section 5.4.3.

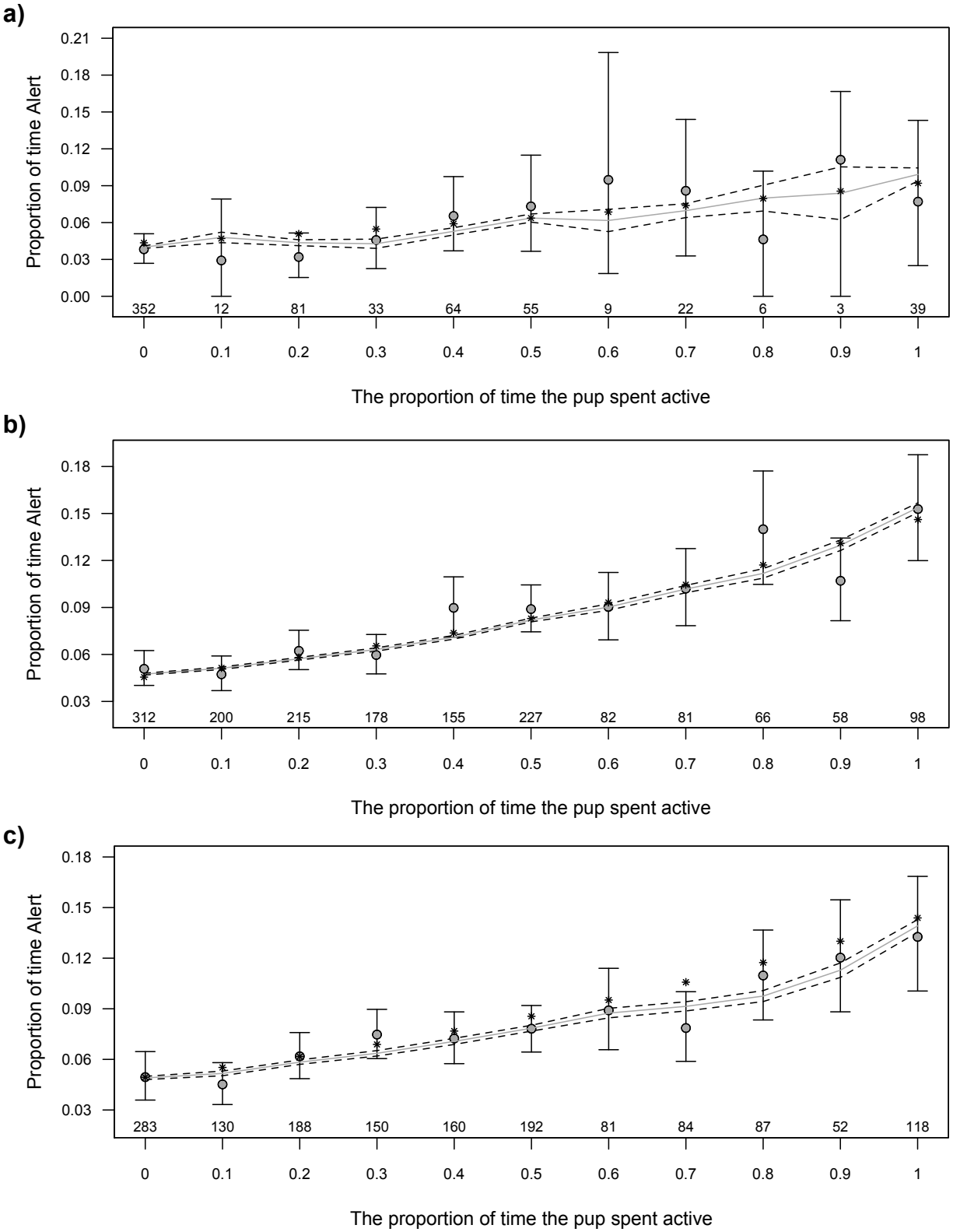


Figure 5.5: The mean observed (grey dots) and the mean fitted (grey line) proportion of time females spent alert in the **a)** 2007 (2007 & 2008 re-sighted individuals) **b)** 2008 and **c)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons across the observed range of pup activity; * indicates the predicted value for each bin of data whilst the other covariates were standardised to their mean. The value on the inside of the x-axis shows the number of data points (hourly scan samples) within the respective bin. The covariates retained in each of these models are noted in Section 5.4.3.

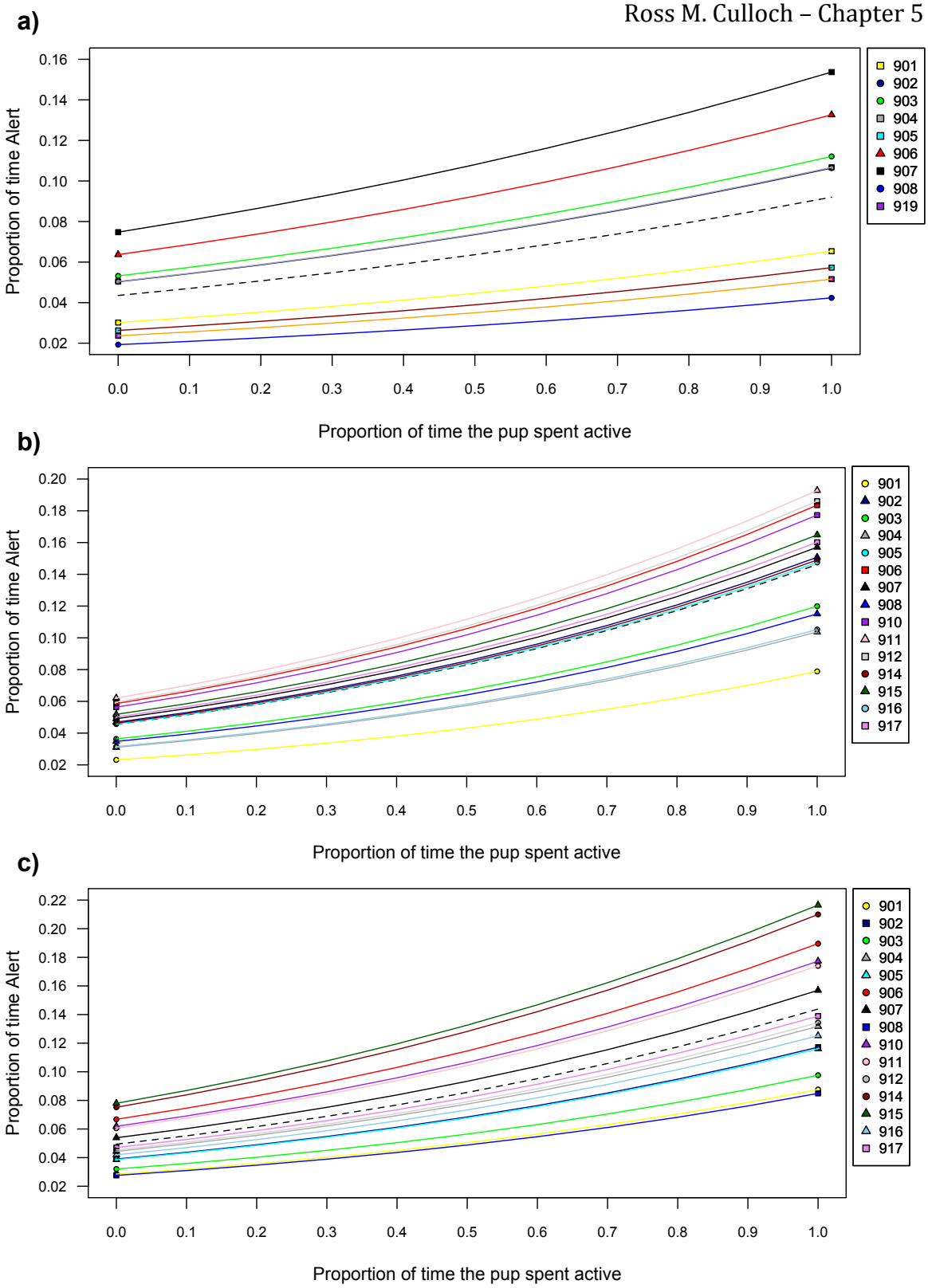


Figure 5.6: The predicted values for the proportion of time each individual spent alert in the **a)** 2007 (2007 & 2008 re-sighted individuals) **b)** 2008 and **c)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons across the observed range of pup activity. The mean of the group is shown as the black dashed line. Each individual has a unique colour code, which is shown in the legend, and is maintained throughout the plots presented in this chapter. The squares, circles and triangles indicate that the sex of the pup was female, male or unknown, respectively.

For each of the re-sighted individuals', the predicted proportion of time spent alert across the observed range of pup activity reiterates the finding that individual variation in this behaviour does occur, and that the proportion of time spent alert increases with pup activity (Figure 5.6). These figures also reiterate that the relationship between the alert behaviour and the activity of the pup is less pronounced for the 2007 datasets (Figure 5.6a). Notably, unlike the pup check behaviour, there are individuals spanning the entire range of between-individual variation; therefore, if an individual were omitted from the group, the influence on the between-individual variation would be minimal. Although data are limited, there is no obvious pattern across the years to suggest that the sex of the pup is influencing a mother's alert behaviour.

5.4.4. Aggression models

There were twenty-one models retained across the six confidence sets for the aggression behavioural category (Table 5.3). Both the individuals' ID and the activity of the pup were retained within thirteen of the models (13/21), and there was varied but limited support for the distance to the nearest female neighbour (7/21), distance to the nearest pool (4/21) and home range usage (2/21). Only the activity of the pup was included in all confidence sets for both the 2008 and 2009 breeding seasons. The individuals' ID and the distance to the nearest female neighbour were retained in the three confidence sets for the 2008 breeding season. The estimated effects for pup activity, the distance to the nearest pool and the distance to the nearest female neighbour were often close to, or less than, twice the standard error. Conversely, despite being retained in relatively few models, the home range usage was the only continuous covariate that was always influential (Table 5.3). Therefore, unlike the pup check and alert behavioural categories, there is no substantial support for any covariate across all confidence sets. Consequently, the simplest model (for the 2008 & 2009 re-sighted individuals) included individuals' ID and pup activity (Table 5.3).

Table 5.3: The summary for each of the models that were retained within the confidence set for individuals that were re-sighted in all three years (2007 - 2009; n = 8), 2007 & 2008 (n = 9), 2008 & 2009 (n = 15) and 2007 & 2009 (n = 9) for the **aggression behavioural category** (the number of models that were retained at each of the 5 stages of the model selection process is shown in Table A5.7). The covariates RAIN and TEMP were not retained in any of the models within the nine confidence sets, and were therefore omitted from the table. See Table 5.1 for the complete table legend, and see the footnote for Table 5.1 for definitions of the covariates and of abbreviations. Table 5.3 is continued overleaf.

						Covariates										
		Intercept		ODC		ACT		NFN		POOL		HOME				
Analyses	Year	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	ID	d.f.	△
2007 - 2009	2008	-4.510	0.621	0.069	0.018	0.890	0.356	0.070	0.042	-	-	-	-	✓	11	0
		-5.178	0.588	0.070	0.018	0.878	0.355	-	-	-	-	-	-	✓	10	0.502
		-4.310	0.626	0.068	0.018	-	-	-0.074	0.043	-	-	-	-	✓	10	4.131
	2009	-4.363	0.389	0.008	0.010	-	-	-	-	-	-	-0.013	0.005	X	3	0
		-5.785	0.295	0.012	0.010	1.066	0.513	-	-	-	-	-	-	X	3	1.414
		-4.909	***0.737***	***0.007***	***0.010***	***-***	***-***	***-***	***-***	***-***	***-***	***-0.011***	***0.006***	✓	***10***	***4.935***
2007 & 2008	2008	-4.575	0.631	0.066	0.017	0.708	0.345	-0.067	0.041	-	-	-	-	✓	12	0
		-4.997	0.546	0.067	0.017	0.762	0.343	-	-	-	-	-	-	✓	11	1.062
		-4.370	0.631	0.066	0.017	-	-	-0.072	0.041	-	-	-	-	✓	11	2.334
		-4.741	0.527	0.066	0.017	-	-	-	-	-	-	-	-	✓	10	3.656

2008 & 2009	2008	-4.400	0.575	0.056	0.012	0.722	0.270	-0.081	0.035	-	-	-	-	✓	18	0
		-4.990	0.531	0.056	0.012	0.742	0.268	-	-	-	-	-	-	✓	17	4.104
		-4.932	0.546	0.056	0.012	0.757	0.267	-	-	-0.032	0.030	-	-	✓	4	5.002
		-4.580	0.149	0.058	0.012	0.952	0.260	-	-	-0.055	0.021	-	-	X	4	5.236
		-4.366	0.195	0.058	0.012	0.943	0.259	-0.087	0.033	-	-	-		✓	17	5.336
	2009	-5.797	0.220	0.016	0.008	0.883	0.336	-	-	0.046	0.014	-	-	X	4	0
		-6.300	0.626	0.014	0.008	1.009	0.351	-	-	-	-	-	-	✓	17	1.394
		-5.104	0.244	0.017	0.008	-	-	-0.051	0.029	0.045	0.014	-	-	X	4	3.231
2007 & 2009	2009	-4.076	0.311	0.028	0.014	-	-	-	-	-	-	-0.014	0.004	X	3	0
		-6.059	0.611	0.028	0.014	0.805	0.458	-	-	-	-	-	-	✓	11	4.924
		-5.522	0.265	0.032	0.014	0.991	0.457	-	-	-	-	-	-	X	3	5.438
		-5.759	0.582	0.029	0.014	-	-	-	-	-	-	-	-	✓	10	5.862

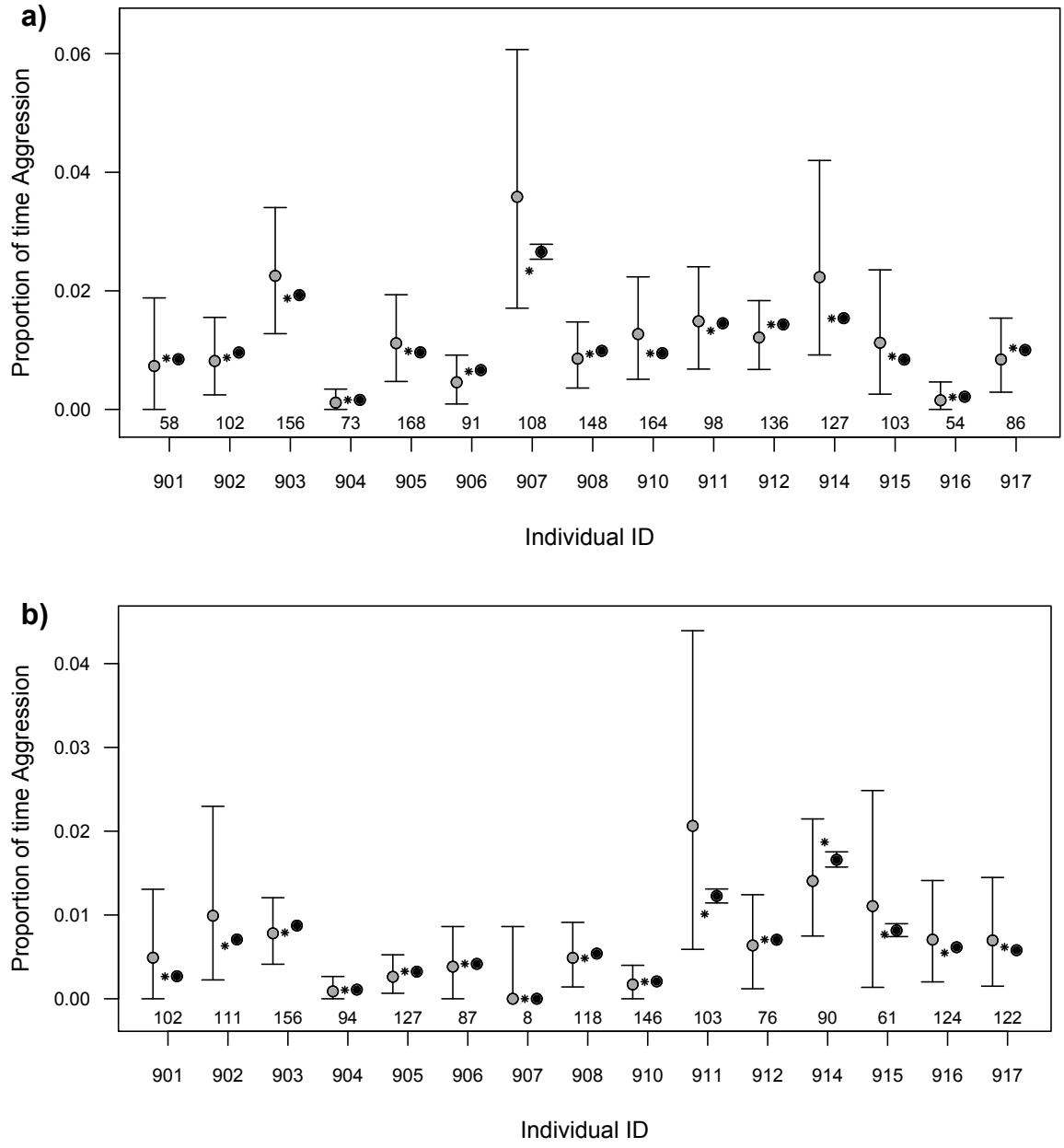


Figure 5.7: The mean observed (grey) and the mean fitted (black) proportion of time that each of the re-sighted individual's spent in the aggression behavioural category in the **a)** 2008 and **b)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons; * indicates the predicted value for each individual whilst the other covariates were standardised their mean. The total number of hours that each individual was observed is noted on the inside of the x-axis. The covariates retained in each of these models are noted in Section 5.4.4.

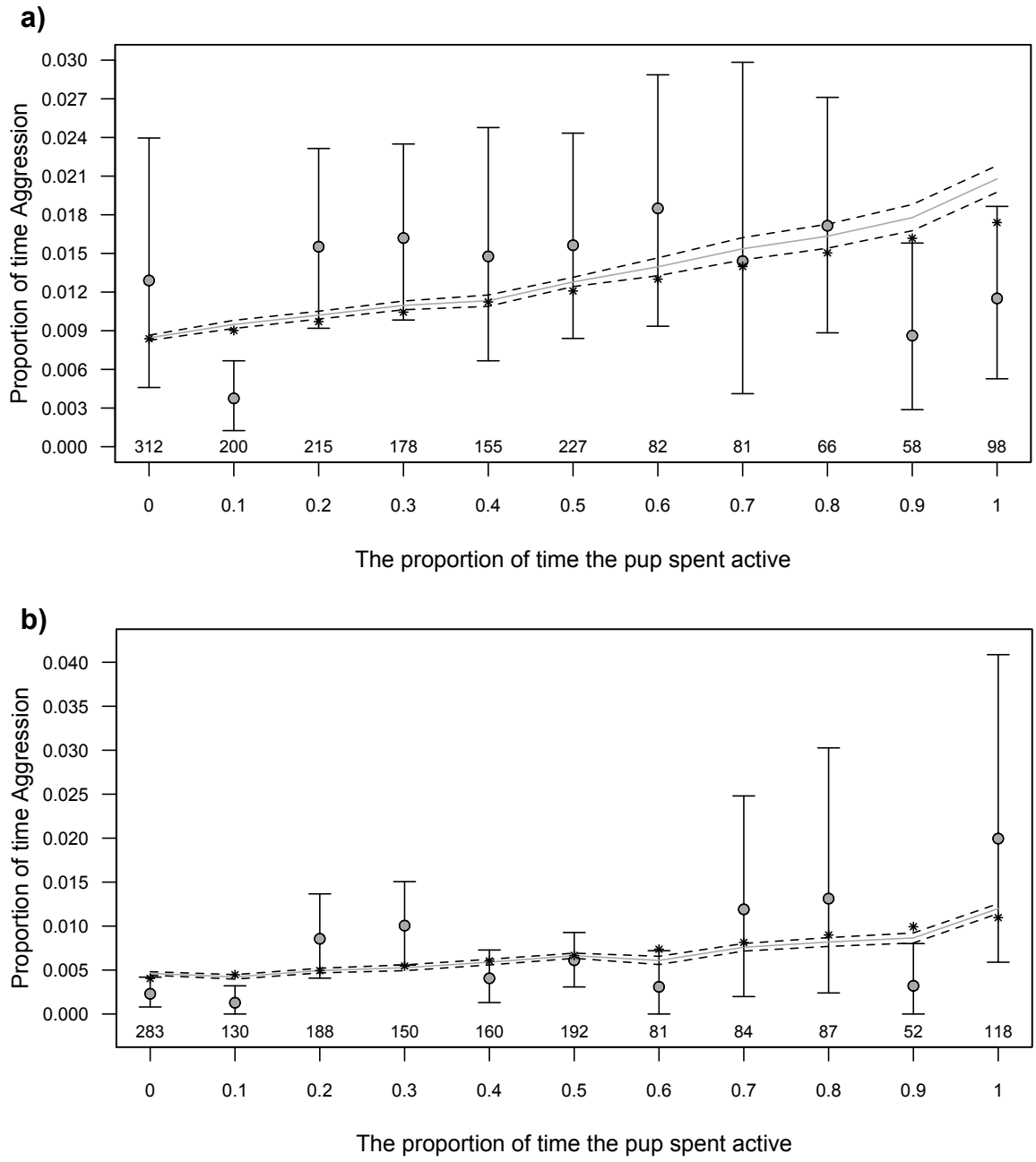


Figure 5.8: The mean observed (grey dots) and the mean fitted (grey line) proportion of time females spent in the aggression behavioural category in the **a)** 2008 and **b)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons across the observed range of pup activity; * indicates the predicted value for each bin of data whilst the other covariates were standardised to their mean. The value on the inside of the x-axis shows the number of data points (hourly scan samples) within the respective bin. The covariates retained in each of these models are noted in Section 5.4.4.

The additional binomial variation did improve the majority of the models (Table 5.3). This is supported by the goodness-of-fit plots, which show that the observed frequency of aggression fitted the beta-binomial distribution well (Figures A5.3). The between- and within-individual variation in the aggression behaviour is evident from the plots of the observed data (Figure 5.7). The model fitted these data well, although similar to both the pup checking and alert behaviours, the within-individual variation was typically less for the fitted values. Where the activity of the pup was standardised to its mean, the accuracy of the predictions in relation to the mean observed and mean fitted values deviated more for some individuals than others.

These models showed that the more active the pup was, the more time the mother spent in the aggression behavioural category (Table 5.3). However, the plots for the fitted and predicted values for pup activity (Figure 5.8) showed that there was considerable variation in the observed data, both within and between bins (which was particularly true for the 2008 dataset). Furthermore, for several bins, the 95% confidence interval for the observed data did not fall within the limits of the 95% confidence interval for the fitted data. Therefore, these models failed to fit the pup activity data; consequently, the plots for the predicted proportion of time that each individual spent in the aggression behavioural category in relation to the activity of their pup are not presented.

5.4.5. Locomotion models

There were nine models retained across the six confidence sets for the locomotion behavioural category (Table 5.4). Individuals' ID was retained in none of the models (0/9), the activity of the pup was retained in the majority of the models (7/9), and there was limited support for the nearest female neighbour (1/9) and home range usage (2/9). The activity of the pup was the only covariate that was retained in all three of the confidence sets for the 2008 and 2009 breeding seasons. Of the continuous covariates retained, only the activity of the pup and the home range usage were considered influential (Table 5.4). However, the simplest model for all datasets retained the activity of the pup, only.

Table 5.4: The summary for each of the models that were retained within the confidence set for individuals that were re-sighted in all three years (2007 - 2009; n = 8), 2007 & 2008 (n = 9), 2008 & 2009 (n = 15) and 2007 & 2009 (n = 9) for the **locomotion behavioural category** (the number of models that were retained at each of the 5 stages of the model selection process is shown in Table A5.7). The covariates RAIN and TEMP were not retained in any of the models within the nine confidence sets, and were therefore omitted from the table. See Table 5.1 for the complete table legend, and see the footnote for Table 5.1 for definitions of the covariates and of abbreviations.

						Covariates										
		Intercept		ODC		ACT		NFN		POOL		HOME				
Analyses	Year	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	ID	d.f.	△
2007 - 2009	2008	-5.957	0.259	<0.001	<0.001	1.870	0.424	-	-	-	-	-	-	X	3	0
		-5.484	***0.538***	***<0.001***	***<0.001***	***2.233***	***0.446***	***-***	***-***	***-0.079***	***0.044***	***-***	***-***	✓	***11***	***6.181***
	2009	-6.033	0.309	0.021	0.013	2.017	0.472	-	-	-	-	-	-	X	3	0
		-3.717	0.305	0.016	0.029	-	-	-	-	-	-	-0.019	0004	X	3	1.336
		-6.681	***0.629***	***0.017***	***0.012***	***2.098***	***0.478***	***-***	***-***	***-***	***-***	***-***	***-***	✓	***10***	***2.941***
2007 & 2008	2008	-5.990	0.250	<0.001	<0.001	1.856	0.409	-	-	-	-	-	-	X	3	0
		-5.428	***0.529***	***<0.001***	***<0.001***	***2.191***	***0.433***	***-***	***-***	***-***	***-***	***-***	***-***	✓	***12***	***7.494***
2008 & 2009	2008	-6.000	0.190	0.002	0.004	1.996	0.316	-	-	-	-	-	-	X	3	0
		-5.564	***0.492***	***0.002***	***<0.001***	***2.086***	***0.330***	***-***	***-***	***-***	***-***	***-***	***-***	✓	***17***	***15.116***
	2009	-5.804	0.197	0.018	0.008	1.974	0.309	-	-	-	-	-	-	X	3	0
		-6.675	***0.618***	***0.014***	***0.008***	***1.940***	***0.319***	***-***	***-***	***-***	***-***	***-***	***-***	✓	***17***	***3.199***
2007 & 2009	2009	-5.561	0.363	0.022	0.012	1.908	0.442	-0.065	0.039	-	-	-	-	X	4	0
		-5.956	0.289	0.023	0.012	1.871	0.444	-	-	-	-	-	-	X	3	1.144
		-3.861	0.278	0.018	0.012	-	-	-	-	-	-	-0.018	0.004	X	3	1.978
		-6.458	***0.679***	***0.019***	***0.012***	***1.983***	***0.448***	***-0.074***	***0.044***	***-***	***-***	***-***	***-***	✓	***12***	***5.410***

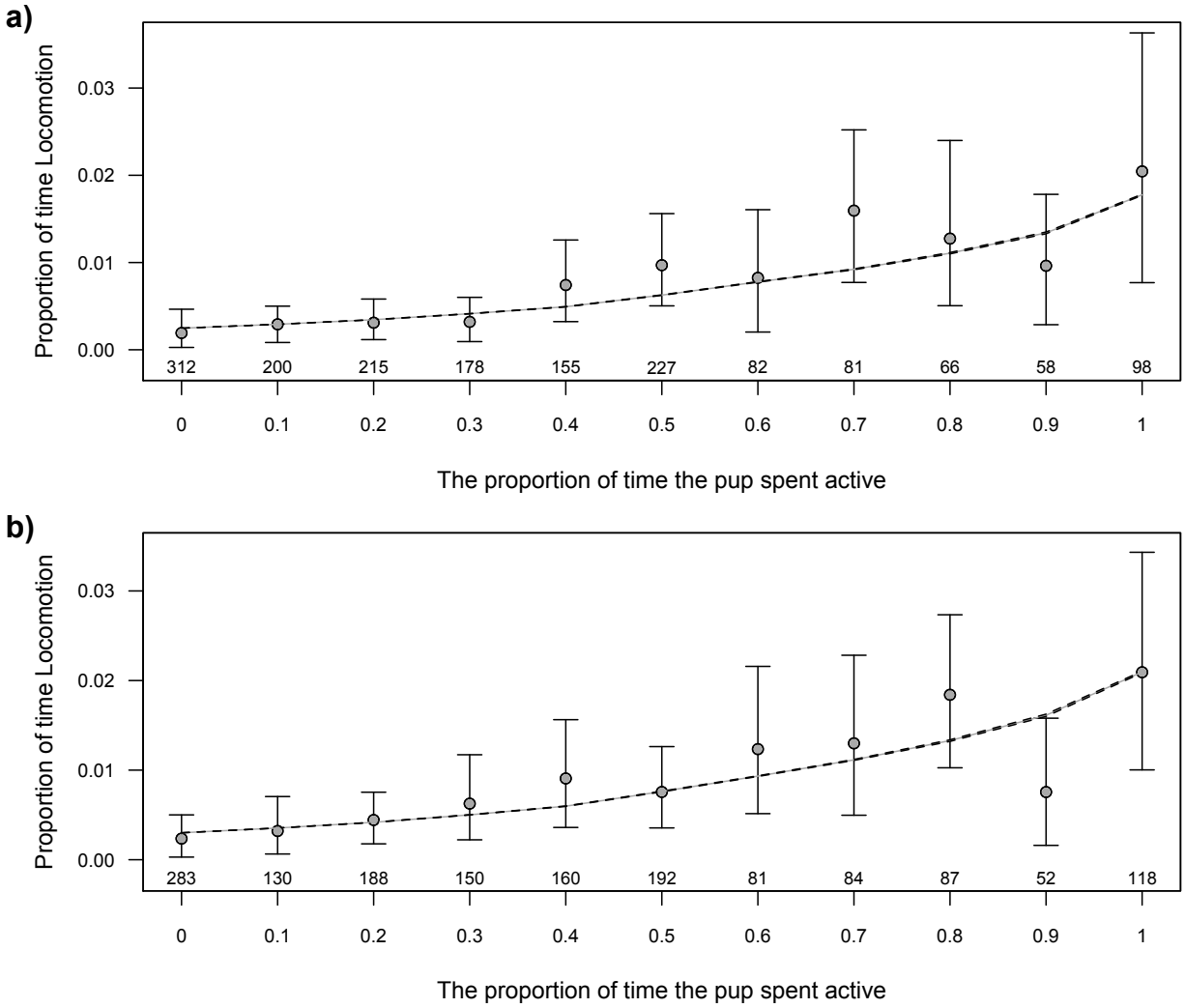


Figure 5.9: The mean observed (grey dots) and the mean fitted (grey line) proportion of time females spent in the locomotion behavioural category in the **a)** 2008 and **b)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons across the observed range of pup activity. There are no predicted values because only one covariate was retained in both of these models. The value on the inside of the x-axis shows the number of data points (hourly scan samples) within the respective bin.

Similar to the pup checking behaviour, the estimate for the overdispersion coefficient was more than twice the standard error for the majority of the models, which indicates that the additional binomial variation did not improve the model. Nevertheless, the goodness-of-fit plots show that the observed frequency of locomotion fitted the beta-binomial distribution well (Figure A5.4). The models showed that the more active the pup was, the more time the mother spent in the locomotion behavioural category (Table 5.4). The models successfully fitted the data to the general trend observed; however, there is considerable variation in the

observed data that was not captured by the model; this is particularly true for higher proportions of time in which the pup spent active (Figure 5.9). There are no predicted values extracted from these models because the activity of the pup was the only influential covariate.

5.5. Discussion

Several of the covariates included in this study were consistently collinear across breeding seasons, and atypical environmental conditions in two of the three breeding seasons were found to heavily influence the relationship between these covariates (Chapter 3, Section 3.14). Consequently, interpreting which covariate(s) is directly influencing behaviour may not be possible. Based on previous publications and the findings presented in Chapter 3, the initial sections below shall provide a biological interpretation of the models retained within the confidence sets for each of the behavioural categories. If collinear covariates offer better and/or additional support to the biological interpretation of these models, then these relationships shall also be considered. Thereafter, the general trends that were found in the models shall be discussed, before comparing the results of the models to the repeatability estimates presented in Chapter 4.

5.5.1. Pup check

The influence of the individuals' ID varied within and between breeding seasons. Where individuals' ID was retained, there was evidence to suggest that one or two individuals considerably influenced the between-individual variation. Consequently, whether or not individuals' ID was retained within a confidence set was heavily dependent upon whether or not these individuals were included in the analyses. The activity of the pup was the only covariate that was retained in all of the confidence sets, and although this covariate was collinear with a number of other covariates, it does make biological sense that the more active the pup was the more likely the mother was to pup check (Fogdon, 1971; Kovacs, 1987; Smiseth & Lorentsen, 1995a, b).

The distance to the nearest pool, which had a significant negative relationship with the distance to the pup, was retained in a third of the models, and had a positive relationship with the pup checking behaviour. Although this covariate was rarely influential, it nevertheless suggests that, the closer the mother was to her pup, the more likely she was to pup check. This may be somewhat confounding, but it does support the supposition that the pup check behaviour is likely to be heavily influenced (either directly or indirectly) by the pup. This is further supported by the 2009 confidence sets, which retained the distance to the nearest pool in all of the 'best' models (two of which had estimates that were considerably influential). This breeding season was both relatively cool and wet (Chapter 3, Section 3.14); consequently, it was hypothesised that a female's need to commute between pup and pool was considerably reduced (Twiss et al., 2000; Redman et al., 2001; Twiss et al., 2002). Therefore, females could remain closer to their pups, which increased the likelihood of females performing pup checks during the 2009 breeding season.

5.5.2. Alert

This was the only behavioural category where individuals' ID was retained in all of the models in all of the confidence sets. Therefore, irrespective of which group of re-sighted individuals was included in the model and/or which breeding season was used in the model, individuals' ID was always retained. Furthermore, individuals did span the majority of the between-individual variation; therefore, the omission of one individual from a group would not substantially reduce between-individual variation. Consequently, this would explain, in part, why individuals' ID was retained in all of the alert models across all nine datasets.

The activity of the pup was retained in the majority of the models, which does make biological sense, such that females with more active pups may need to be more aware of their immediate surroundings (Pomeroy et al., 1994; Twiss et al., 2000). However, the activity of the pup has a significant, negative relationship with the home range usage for all but the 2007 re-sighted individuals' datasets. In this instance, the models show that the closer the individual is to the centre of the core area of their home range, the less alert they are. Or, in other words, females

are more alert in less familiar geographic locations. However, the home range was included in the global model, but was not retained in the confidence set for either the 2008 or 2009 breeding seasons. Therefore, if the home range did influence behaviour, it had a considerably smaller effect than the activity of the pup.

5.5.3. Aggression

Previous studies have regularly used aggression to test for CIDs in the laboratory and in the field (Huntingford, 1976; Sih et al., 2004; Kraji-Fisher et al., 2007). In the present study, there was some evidence to suggest that individual identity did explain some of the variation in the aggression behavioural category. However, the other influential covariates retained within the simplest models poorly explained the additional variation in this behaviour. One explanation for this outcome is that influential covariates were omitted from the models (Crawley, 2007). Aggression has been shown to influence the distribution and density of known individuals whilst on the breeding colony (Stephenson et al., 2007). These spatial patterns in aggression may be influenced by social affiliations, which are known to exist within some areas of the North Rona breeding colony (Pomeroy, et al., 2005). Therefore, the identity of the nearest female neighbour and/or the social stability of affiliations across breeding seasons (Ruddell et al., 2007) may need to be included in these models in order to accurately predict aggressive behaviour.

5.5.4. Locomotion

As expected, the variation in the locomotion behavioural category was best explained by the social and environmental covariates. There was considerable variation in the confidence intervals for the observed data, particularly for higher proportions of time in which the pup spent active. This may be due to the fact that locomotion accounted for the smallest percentage of an individual's activity budget (median percentage of time spent = 0.65%; Chapter 3, Table 3.1); nevertheless, the models predicted these data relatively well. The activity of the pup (which was the most influential covariate) had a positive relationship with locomotion. However, as noted previously, the pup activity has a significant, negative relationship with home range usage for the 2008 and 2009 breeding seasons.

Therefore, the closer an individual was to the centre of the core area of their home range, the less likely they were to move, which would be expected. The global model did include home range usage, and it was retained in two of the three confidence sets for the 2009 breeding season, both of which were influential; however, in both instances the model retaining pup activity had a lower AICc. Therefore, there was evidence to suggest that home range usage may have influenced locomotion; however, the activity of the pup appears to have had a considerably greater effect.

5.5.5. General trends in the data

The effect of the sampling protocol used in 2007 was evident in the pup check and alert behavioural categories, where variation in the observed and fitted values tended to be greater. Furthermore, trends in the data that were clearly shown in the 2008 and 2009 breeding seasons were less pronounced in the 2007 breeding season. Therefore, the smaller sample sizes in 2007 may have influenced the models' ability to fit these data (Chapter 2, Section 2.5.4). For the aggression and locomotion behavioural categories (which were infrequently recorded), it was not possible to model the 2007 datasets because there were too few occurrences of these behaviours for some individuals. Therefore, in order to obtain sufficient data to model these behaviours, and to accurately model both the pup check and alert behaviours, it appears that an intensive observational approach is required. The suitability of the sampling protocols used in this thesis for each of the eight behavioural categories was discussed in Chapter 2, Section 2.5.4 and shall be discussed further in Chapter 9.

The 95% confidence intervals for the observed values were often considerably greater than the 95% confidence intervals for the fitted values. Given that the observed data are comprised of a maximum of 12 data points (i.e. 12 five minute scans in one hour), these data points will be prone to outliers, particularly if the number of scan samples per hour is low (Chapter 3, Section 3.11). Therefore, using the conventional 95% confidence interval with these data will give wider confidence intervals for the observed data. Conversely, the fitted values will give

comparably smaller confidence intervals, because the GLM will give less weight to these outliers (Crawley, 2007).

The accuracy of the predicted values (with respect to the mean observed and mean fitted values), for the Individuals' ID and the activity of the pup were variable for both the pup check and alert behavioural categories. However, the results presented in this chapter showed that taking the mean proportion of time spent in the given behaviour by the group of re-sighted individuals (i.e. standardising individuals' ID to its mean) is likely to result in poorer estimates, simply because an 'average' mother is unlikely to be representative of a given individual. Although it was not addressed here, based on the individual variation in behaviour shown for the females; the behaviour of an 'average' pup is also unlikely to be representative of a given individual. Furthermore, some studies have shown that differential investment between the sexes does occur in grey seals (e.g. Kovacs & Lavigne, 1986a; Anderson & Fedak, 1987; Kovacs, 1987; Baker et al., 1995). Therefore, the sex of the pup (as well as the pup's behaviour) may also influence the repeatability of the mothers' behaviour. However, other studies have provided evidence against differential investment (e.g. Bowen et al., 1992; Smiseth & Loensten, 1995b; Pomeroy et al., 1999), and although data were few, in the present study, there was no evidence that pup sex influenced the pup check or the alert behaviours.

5.5.6. Comparison of ICC and GLM results

There are some clear similarities between the results of the GLM analyses presented here, and the ICC analyses presented in Chapter 4. In particular, where the alert behaviour was repeatable in all four of the ICC analyses, individuals' ID was retained in every model within the confidence set for all nine of the GLM analyses. The pup check behaviour was only repeatable for the individuals that were re-sighted in 2008 & 2009, and in the GLM analyses individuals' ID (with respect to the cross-comparison between breeding seasons for re-sighted individuals), was only retained within the confidence sets for those individuals that were re-sighted in 2008 & 2009. The ICCs gave unconvincing support for repeatability in aggression, and the GLMs also showed a similarly unconvincing

pattern, such that individuals' ID (for the 2008 and 2009 re-sighted individuals' datasets) was not retained in all of the models pertaining to the repeatable datasets in Chapter 4. For the locomotion behavioural category, which was not repeatable in any of the ICC analyses, the GLMs showed that covariates other than individuals' ID best explained the variance in this behaviour. For three of the four behaviours analysed in this chapter, there is evidence to suggest that individuals' ID does influence behaviour, which is particularly true for the alert behavioural category. However, using this analytical approach, it is not possible to quantify whether or not the individual variation within breeding seasons is consistent across breeding seasons. In order to do this, these data have to be analysed using Generalised Linear Mixed Models (GLMMs), which shall be carried out in the subsequent chapter.

Chapter Six:
The application of Generalised Linear Mixed Models to address whether or not consistent individual differences in behaviour occur across breeding seasons

6.1. Introduction

Ecological data (and arguably more so, behavioural data) are often subject to unavoidable phenomenon which violate a number of statistical assumptions if they are not suitably dealt with (Zuur et al., 2009b). These include zero inflation, overdispersion, collinearity of covariates and (temporal and spatial) autocorrelation; all of which have been discussed in Chapter 3, in relation to the data presented in this thesis. Despite many of these analytical caveats, as ecologists we often ask and attempt to answer increasingly more complex questions, and as a consequence we look to rapidly evolving analytical techniques such as Generalised Linear Mixed Models (GLMMs) to aid us in answering these questions (Bolker, 2008; Bolker et al., 2009; van de Pol & Wright, 2009; Zuur et al., 2009b; Wilson et al., 2010; Martin et al., 2011). However, in haste to apply such cutting-edge techniques, coupled with the ease in which statistical software allows researchers to apply mixed-models, more and more ecologists are ignoring and/or misinterpreting the assumptions and/or the limitations of these analytical techniques (Bolker, 2008; Bolker et al., 2009; Zuur et al., 2009b). For example, a literature review by Bolker et al. (2009) found that 58% (n = 537 analyses in 200 publications) of peer-reviewed papers in ecological and/or evolutionary journals incorrectly applied GLMMs. Therefore, it is fundamentally important that researchers are aware of the issues pertaining to such analytical techniques prior to applying them, and that they acknowledge where their data do not meet these assumptions and/or limitations.

6.2. Generalised Linear Mixed Models

The principal difference between fixed-effects models and mixed-effects models are that the latter incorporates both fixed effects (which are parameters that are associated with an entire population or with certain repeatable levels of

experimental factors), and random effects (which are associated with individual experimental units drawn at random from a population; Pinheiro & Bates, 2000). Whether or not a covariate is regarded as fixed or random depends on whether inference is to be made about particular levels of a categorical covariate (for example, individuals in a population) or whether inference is to be made about the population from which these levels (individuals) are drawn. In the former, the covariate would be fixed (e.g. GLM) and in the latter, random (e.g. GLMM). Therefore, by including a covariate as a fixed effect, inference is made on the specific differences across the means from one individual to the next. Conversely, by including a covariate as a random effect, inference is made on the extent to which the variation that is not captured by the fixed effects is caused by differences between individuals within the population. Consequently, the random effect indicates the variance within the population, and therefore provides information on the degree of heterogeneity of individuals (Pinheiro & Bates, 2000; Crawley, 2007; Zuur et al., 2009b).

An estimate for each level of a random effect can be extracted from a GLMM. These are often referred to as best linear unbiased predictors (BLUPs), which provide estimates of random effects independent of the other terms within the model. In other words, the BLUP represents the variation for individual *x*, which has not been captured by the explanatory covariates included in the model (Pinheiro & Bates, 2000; Kruuk, 2004; Crawley, 2007; Everitt & Hothorn, 2011). BLUPs were initially developed for (and are still commonly used for), predicting the expected phenotype of an animal's offspring using an individual's breeding value (Robinson, 1991, Hadfield et al., 2010; Morrissey et al., 2010; Wilson et al., 2010). However, BLUPs are also used as a more general method for predicting random effects in a variety of fields (Robinson, 1991), including behavioural ecology (e.g. Kruuk, 2004; Boon et al., 2007; Dingemanse et al., 2007; Boon et al., 2008; Martin & Réale, 2008a, b; Magnhagen & Bunnefeld, 2009; Minderman et al., 2009; Moyes et al., 2009). Therefore, BLUPs can be used to provide an estimated effect for individual *x*, once the influence of the fixed effects has been accounted for.

6.3. Aims

The principal aim of this chapter is to ascertain whether or not consistent individual differences (CIDs) in behaviour do occur across breeding seasons, once the effect of other covariates (which are known to influence behaviour), have been accounted for. As was done in Chapter 5, each breeding season for each group of re-sighted individuals shall be modelled separately (i.e. a total of nine datasets: three for 2007 - 2009; two for 2007 & 2008; two for 2008 & 2009; two for 2007 & 2009). Using GLMMs, the BLUPs for each individual shall be extracted from the simplest model in each of the confidence sets. The intraclass correlation coefficient (ICC; Chapter 4) shall then be used to estimate the repeatability between the BLUPs for the same groups of re-sighted individuals. Furthermore, the BLUPs of re-sighted individuals shall be compared across all combinations of the models retained within the confidence sets to assess how robust these repeatability estimates are. As the data presented in Chapter 5 do not strictly conform to all of the assumptions and/or limitations of GLMMs, it shall be stated clearly throughout where these assumptions are not met and/or where the limitations of the analyses are ignored.

6.4. Methods

Much of the analyses presented in this chapter are from a rapidly evolving field of ecological statistics. Therefore, the information and/or advice required in order to carry out some of these analyses comes from either personal communications with leading experts in the field, or from reading responses to questions previously posted by these individuals, on the board of the R-sig-mixed-models group (https://stat.ethz.ch/mailman/listinfo/r-sig-mixed-models). In the text, where a name and date are cited, this refers to a post that is available on the R-sig-mixed-models groups' website (and with the cited information, the original post can be sourced).

6.4.1. The response and explanatory variables

The analyses presented in this chapter used the same datasets as used in Chapter 5. In this chapter, only the pup check and the alert behavioural categories are modelled. These behavioural categories were selected for three reasons: 1) the GLMs presented in Chapter 5 fitted the data well, 2) individuals' ID was retained in the models for at least one of the four groups of re-sighted individuals', 3) the GLMs supported the findings of the ICCs in Chapter 4 (see Chapter 5, Section 5.5.6). The Individuals' ID was included in the GLMMs as a random effect, whilst all other covariates were included as fixed effects (see Chapter 5, Section 5.3.4 for information on each of the covariates).

6.4.2. Approximating likelihood and model selection

The fixed and random effects of a GLMM are fitted by maximum likelihood (Pinherio & Bates, 2000; Bolker et al., 2009; Zuur et al., 2009b). Although there are a number of ways in which to approximate the likelihood in order to estimate the GLMM parameters; in the present study, following Bolker et al.'s (2009) guidelines, the laplace approximation was used. For model selection, the five-step model selection process as detailed in Chapter 5, Section 5.3.6 was used. However, because there is no agreed method for calculating the degrees of freedom for a GLMM (which are required in order to calculate the AICc; Bolker et al., 2009), the AIC was used for model selection. Given that inference on the confidence sets for the GLM analyses (Chapter 5) did not change irrespective of whether the AIC or the AICc was used (data not presented), this was not considered to be an issue. To visually assess the goodness-of-fit, the predicted values were extracted from the simplest GLMMs and were plotted against the observed values (see Chapter 5, Section 5.3.8).

6.4.3. Quantifying the importance of the random effects

There is much discussion about testing the significance of random effects. Most recently Bolker et al. (2009) note that without being able to calculate the number of degrees of freedom, it is difficult to calculate these *p* values (see also

Bolker's wikidot webpage: http://glmm.wikidot.com/random-effects-testing for more details). Despite these mathematical issues, it is argued that the inclusion of random effects in a model should be considered as part of the experimental design. Therefore, irrespective of the variance explained and/or whether the random effect is considered significant or not, it should be retained in the model (Bolker, 11th March 2010; Renwick, 11th March, 2010; Simpson, 11th October 2011). In the case of the present study, by using AIC as opposed to null hypothesis significance testing (NHST), this point can be considered moot, as analytical paradigms should not be mixed (Burnham et al., 2011; see also Chapter 5, Appendix, Section B). However, by using AIC, one may be tempted to compare the GLM (without individuals' ID) to the GLMM and thus quantify the relative importance of individuals' ID. However, it is not possible to compare the two models because the relevant weighting of the covariates are different between these two modelling approaches (Maindonald, 26th May 2011; Bolker, pers. com.). Therefore, in the present study the importance of the random effect (individuals' ID), shall not be quantified nor shall it be removed from the model, irrespective of the amount of variance it explains.

6.4.4. Overdispersion

The GLMM analyses were carried out in R using the command glmer() in the *lme4* package (Bates et al., 2011). One limitation of this package is that for binomial data there are no distributions available to deal with non-normal, overdispersed data. Therefore, in order to carry out these analyses in the *lme4* package, the binomial (B) distribution had to be used. For the pup check behavioural category this is not a problem; despite the beta-binomial (BB) distribution being used for the GLM analyses, the comparison between the B and the BB distributions showed that the former generally fit the pup check data better than the latter (Chapter 5, Appendix, A5.1 and A5.2). However, for the alert behavioural category, the BB distribution fit the data considerably better than the B distribution (Chapter 5, Appendix, A5.1 and A5.2). To test for overdispersion, the sum of the squared Pearson residuals extracted from the simplest model shall be presented, and these values should be χ^2 distributed (otherwise the data are

overdispersed; Bolker et al., 2009). However, there is no rule of thumb which states how much greater than 1 this value can be before overdispersion becomes an issue. For example, Richards (2008) considers 1.22 as a weak indication of overdispersion, and Crawley (2007) considers 1.95 as strong indication of overdispersion. Nevertheless, for the GLMM analyses presented here it is acknowledged that using the B distribution with the alert behavioural data could potentially lead to serious problems (Hinde & Demétrio, 1998; Burnham & Anderson, 2002; Richards, 2008), which shall be discussed later.

6.4.5. Best linear unbiased predictors of the random effects

The BLUPs were extracted from all of the models retained within the nine confidence sets for both of the behavioural categories. The repeatability of the BLUPs for each of the re-sighted individuals from the pairwise (2007 & 2008; 2008 & 2009; 2007 & 2009) and all three (2007 - 2009) breeding seasons were assessed using the ICC (Chapter 4, Section 4.3). Given that any one of the models within the confidence sets could be the 'best' model (Burnham & Anderson, 2002; Richards, 2005; Bolker, 2008), it was considered prudent to assess whether the repeatability between these models was robust. Therefore, repeatability was assessed for all combinations of the models retained within the confidence sets for each group of re-sighted individuals. Only repeatability estimates that are significant ($p \leq 0.05$) shall be considered. The ICC analyses were carried out in R using the command ICC() available in the package *psych* (Revelle, 2011).

6.5. Results

The number of models retained at each of the five stages of the model selection process is shown in Table A6.1. Collinearity between covariates occurred in 11 of the 18 confidence sets. For each of the datasets, the number of models retained from a possible 63, ranged between 1 and 5 (median = 2). The estimated dispersion parameter for the simplest models for each of the nine datasets for the pup check and alert behaviours ranged between 0.765 - 1.128, and 1.121 - 1.463, respectively (Table A6.2). All of the models that were retained

within the confidence sets for both of the behavioural categories shall be presented in the model tables. Only the △ values are presented in these tables, as the AIC values themselves are uninformative (Bolker, 2008).

6.5.1. Goodness-of-fit

The goodness-of-fit plots for the pup check behaviour showed that the observed frequency fitted the binomial distribution well (Figure A6.1). For the alert behaviour, the plots showed that the observed frequency fitted the binomial distribution reasonably well for observed occurrences ≤ 1; however, the model typically failed to predict observed occurrences that were > 1 (Figure A6.2). In the following sections, inference shall be made on the simplest models retained within the nine confidence sets for the pup check and alert behaviour. The potential issues regarding the goodness-of-fit plots for the alert behavioural category shall be raised in the discussion.

6.5.2. Pup check

There were 18 models retained across the 9 confidence sets for the pup check behavioural category. Across all 18 models, the estimated variance of the individuals' ID ranged from < 0.001 to 0.381 (Table 6.1). The estimates for the 2007 datasets were comparably larger than those for 2008 and 2009, which, with the exception of the 2008 & 2009 re-sighted individuals' datasets, generally had variance estimates of ca. 0. The activity of the pup was retained in all of the models in all of the confidence sets (18/18), and there was some support for distance to the nearest pool (5/18), the distance to the nearest female neighbour (3/18) and rainfall (2/18). Between datasets, both the nearest female neighbour and rainfall covariates had a positive and a negative relationship with the pup check behaviour, which is likely to indicate the influence of collinear covariates that were omitted from the models.

With the exception of the activity of the pup, the only other covariate that was retained in the three confidence sets for the same breeding season was the distance to the nearest pool in 2009. Furthermore, in all three of the 2009

Table 6.1: The summary for each of the models that were retained within the confidence set for individuals that were re-sighted in all three years (2007 - 2009; n = 8), 2007 & 2008 (n = 9), 2008 & 2009 (n = 15) and 2007 & 2009 (n = 9) for the **pup check behavioural category** (the number of models that were retained at each of the 5 stages of the model selection process is shown in Table A6.1). The models are arranged using the △ value; the AIC value is not presented. If the covariate was retained within the model then the estimated effect (Est.) and the standard error of the estimate (SE) are included in the table. ID was included as a random effect; the variance explained (var.) and the standard deviation (SD) are included in the table. See the footnote for definitions of the covariates. The covariates HOME and TEMP were not retained in any of the models within the nine confidence sets, and were therefore omitted from the table. The model number (No.) relates to the ICC analyses (Tables A6.3); the simplest models for each confidence set are in bold. The simplest models for the individuals' re-sighted in 2008 & 2009 are plotted in Figure 6.1. Table 6.1 is continued overleaf.

					Covariates										
			Intercept		**ID**		**ACT**		**NFN**		**POOL**		**RAIN**		
Analyses	**Year**	**No.**	**Est.**	**SE**	**Var.**	**SD**	**Est.**	**SE**	**Est.**	**SE**	**Est.**	**SE**	**Est.**	**SE**	△
2007 – 2009	2007	**1**	**-4.129**	**0.230**	**0.187**	**0.432**	**1.333**	**0.361**	**-**	**-**	**-**	**-**	**-**	**-**	**0**
	2008	1	-4.713	0.162	0.004	0.062	1.258	0.255	-	-	0.027	0.015	-	-	0
		2	**-4.586**	**0.143**	**0.004**	**0.060**	**1.263**	**0.255**	**-**	**-**	**-**	**-**	**-**	**-**	**1.088**
	2009	**1**	**-4.962**	**0.176**	**<0.001**	**<0.001**	**1.394**	**0.271**	**-**	**-**	**0.037**	**0.012**	**-**	**-**	**0**
		2	-5.053	0.223	0.046	0.214	1.500	0.277	0.040	0.018	-	-	-	-	5.010
2007 & 2008	2007	1	-3.978	0.347	0.338	0.582	1.417	0.356	-0.084	0.058	-	-	-	-	0

		2	**-4.336**	**0.270**	**0.381**	**0.617**	**1.442**	**0.358**	**-**	**-**	**-**	**-**	**-**	**-**	**0.322**
	2008	1	-4.705	0.151	<0.001	<0.001	1.263	0.243	-	-	0.025	0.014	-	-	0
		2	**-4.597**	**0.136**	**<0.001**	**0.027**	**1.274**	**0.243**	**-**	**-**	**-**	**-**	**-**	**-**	**0.848**
2008 & 2009	2008	1	-4.506	0.136	0.075	0.274	1.617	0.177	-	-	-	-	-0.017	0.012	0
		2	**-4.600**	**0.122**	**0.076**	**0.275**	**1.630**	**0.176**	**-**	**-**	**-**	**-**	**-**	**-**	**0.293**
	2009	1	-4.606	0.161	0.143	0.379	1.382	0.178	-	-	0.023	0.011	-	-	0
		2	-4.524	0.145	0.127	0.357	1.376	0.178	-	-	-	-	0.017	0.009	0.689
		3	**-4.453**	**0.144**	**0.145**	**0.381**	**1.398**	**0.178**	**-**	**-**	**-**	**-**	**-**	**-**	**2.428**
2007 & 2009	2007	**1**	**-4.106**	**0.209**	**0.153**	**0.391**	**1.234**	**0.347**	**-**	**-**	**-**	**-**	**-**	**-**	**0**
	2009	1	-4.999	0.171	<0.001	<0.001	1.478	0.261	-	-	0.030	0.012	-	-	0
		2	-5.154	0.219	0.052	0.228	1.580	0.266	0.042	0.018	-	-	-	-	1.575
		3	**-4.865**	**0.167**	**0.013**	**0.115**	**1.595**	**0.263**	**-**	**-**	**-**	**-**	**-**	**-**	**4.077**

ID: Individuals' identification code (entered as a random effect); **ACT**: proportion of time the pup spent active; **NFN**: the distance between a mother and her nearest female neighbour (m); **POOL**: the distance between a mother and her nearest pool (m); **HOME**: the location of the female within her estimated home range (Kernel Density Estimate), which ranges from 1 - 100, where 100 is the centre of the core area of the home range; **RAIN**: the volume of rain that fell from the end of observations on day *x* and the end of observations on day *x*+1 (mm); **TEMP**: air temperature (^{o}C); With the exception of rainfall (which was recorded daily) the other spatial and environmental covariates were recorded at hourly intervals.

confidence sets, the distance to the nearest pool was retained in the 'best' model and was influential. However, in most models, the distance to the nearest pool, the distance to the nearest female neighbour and rainfall, were typically close to, or less than, twice the standard error (Table 6.1). Consequently, for the majority of the datasets, the simplest model included pup activity, only. The one exception was the 2009 model from the 2007 - 2009 re-sighted individuals' datasets, where the simplest model with the lowest AIC included pup activity and distance to the nearest pool (Table 6.1).

Only the BLUPs extracted from the simplest models for the individuals re-sighted in 2008 & 2009 were repeatable (ICC2 = 0.71, F = 5.6, p = 0.001, n = 15; Table 6.3; Figure 6.1). Nevertheless, the repeatability estimates for these re-sighted individuals were robust to all possible combinations of the BLUPs extracted from the models retained within the respective confidence sets (Table A6.3). Of the other three groups of re-sighted individuals, no combination of BLUPs extracted from the models within the respective confidence sets yielded a significant repeatability estimate (Table A6.3).

6.5.3. Alert

There were 17 models retained across the 9 confidence sets for the alert behavioural category. Across all 17 models, the estimated variance of the individuals' ID ranged from 0.054 to 0.225 (Table 6.2). The activity of the pup was retained in all of the models in all of the confidence sets (17/17), and there was some support for distance to the nearest pool (3/17), nearest female neighbour (4/17), home range usage (1/17) and rainfall (3/17). With the exception of the activity of the pup, the other covariates that were retained in all three of the confidence sets for the same breeding season were the nearest female neighbour and rainfall in 2008, and the distance to the nearest pool in 2007. Across the nine confidence sets, only one of the covariates had an estimated effect that was less than twice the standard error (2007 - 2009 nearest female neighbour in 2008, estimate = 0.027, SE = 0.015). Nevertheless, the simplest model across the majority of datasets included pup activity, only. The two exceptions were the 2009 model from the 2007 - 2009 re-sighted individuals' datasets, where the simplest

Table 6.2: The summary for each of the models that were retained within the confidence set for individuals that were re-sighted in all three years (2007 - 2009; n = 8), 2007 & 2008 (n = 9), 2008 & 2009 (n = 15) and 2007 & 2009 (n = 9) for the **alert behavioural category** (the number of models that were retained at each of the 5 stages of the model selection process is shown in Table A6.1). The models are arranged using the △ value; the AIC value is not presented. If the covariate was retained within the model then the estimated effect (Est.) and the standard error of the estimate (SE) are included in the table. ID was included as a random effect; the variance explained (var.) and the standard deviation (SD) are included in the table. See the footnote of Table 6.1 for definitions of the covariates. The covariate TEMP was not retained in any of the models within the nine confidence sets, and was therefore omitted from the table. The model number (No.) relates to the ICC analyses (Tables A6.4); the simplest models for each confidence set are in bold. The simplest models for all four groups of re-sighted individuals' are plotted in Figures 6.2 - 6.5. Table 6.2 is continued overleaf.

					Covariates												
			Intercept		**ID**		**ACT**		**NFN**		**POOL**		**HOME**		**RAIN**		
Analyses	**Year**	**No.**	**Est.**	**SE**	**Var.**	**SD**	**Est.**	**SE**	**Est.**	**SE**	**Est.**	**SE**	**Est.**	**SE**	**Est.**	**SE**	△
2007 – 2009	2007	1	-3.359	0.207	0.156	0.395	0.890	0.256	-	-	0.131	0.053	-	-	-	-	0
		2	**-3.117**	**0.176**	**0.149**	**0.387**	**0.885**	**0.258**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**3.830**
	2008	1	-3.012	0.122	0.057	0.239	1.151	0.136	-	-	-	-	-	-	-0.022	0.009	0
		2	-3.280	0.139	0.058	0.241	1.175	0.136	0.027	0.015	-	-	-	-	-	-	2.026
		3	**-3.132**	**0.111**	**0.054**	**0.232**	**1.173**	**0.136**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**2.029**
	2009	**1**	**-2.728**	**0.183**	**0.057**	**0.238**	**1.181**	**0.151**	**-**	**-**	**-**	**-**	**-0.007**	**0.002**	**-**	**-**	**0**
2007 & 2008	2007	1	-3.428	0.203	0.176	0.419	0.845	0.253	-	-	0.138	0.053	-	-	-	-	0

		2	**-3.178**	**0.175**	**0.173**	**0.416**	**0.840**	**0.254**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**4.556**
	2008	**1**	**-3.151**	**0.178**	**0.212**	**0.460**	**1.126**	**0.135**	**-**	**-**	**-**	**-**	**-**	**-**	**-0.023**	**0.009**	**0**
		2	-3.460	0.194	0.225	0.474	1.158	0.135	0.032	0.015	-	-	-	-	-	-	2.320
2008 & 2009	2008	1	-3.205	0.098	0.058	0.242	1.265	0.097	0.028	0.011	-	-	-	-	-	-	0
		2	-2.989	0.086	0.055	0.235	1.259	0.097	-	-	-	-	-	-	-0.014	0.006	1.007
		3	**-3.066**	**0.080**	**0.056**	**0.236**	**1.271**	**0.100**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**4.292**
	2009	**1**	**-3.045**	**0.104**	**0.112**	**0.335**	**1.218**	**0.102**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**0**
2007 & 2009	2007	1	-3.276	0.186	0.132	0.363	0.723	0.247	-	-	0.112	0.051	-	-	-	-	0
		2	**-3.082**	**0.160**	**0.132**	**0.363**	**0.727**	**0.248**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**2.589**
	2009	**1**	**-3.348**	**0.137**	**0.099**	**0.314**	**1.271**	**0.144**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**0**

model included pup activity and home range usage; and the 2008 model from the 2007 & 2008 re-sighted individuals' datasets, where the simplest model with the lowest AIC included pup activity and rainfall (Table 6.2).

All the BLUPs extracted from the simplest models for all of the groups of re-sighted individuals were repeatable (Table 6.3; Figures 6.2 - 6.5). Furthermore, the majority of these repeatability estimates were robust to all possible combinations of the BLUPs extracted from the models within the respective confidence sets (Table A6.4). However, there was one exception (from 15 analyses) where the repeatability estimate was not significant (2007 & 2009, ICC2 = 0.55, F = 3.2, p = 0.062).

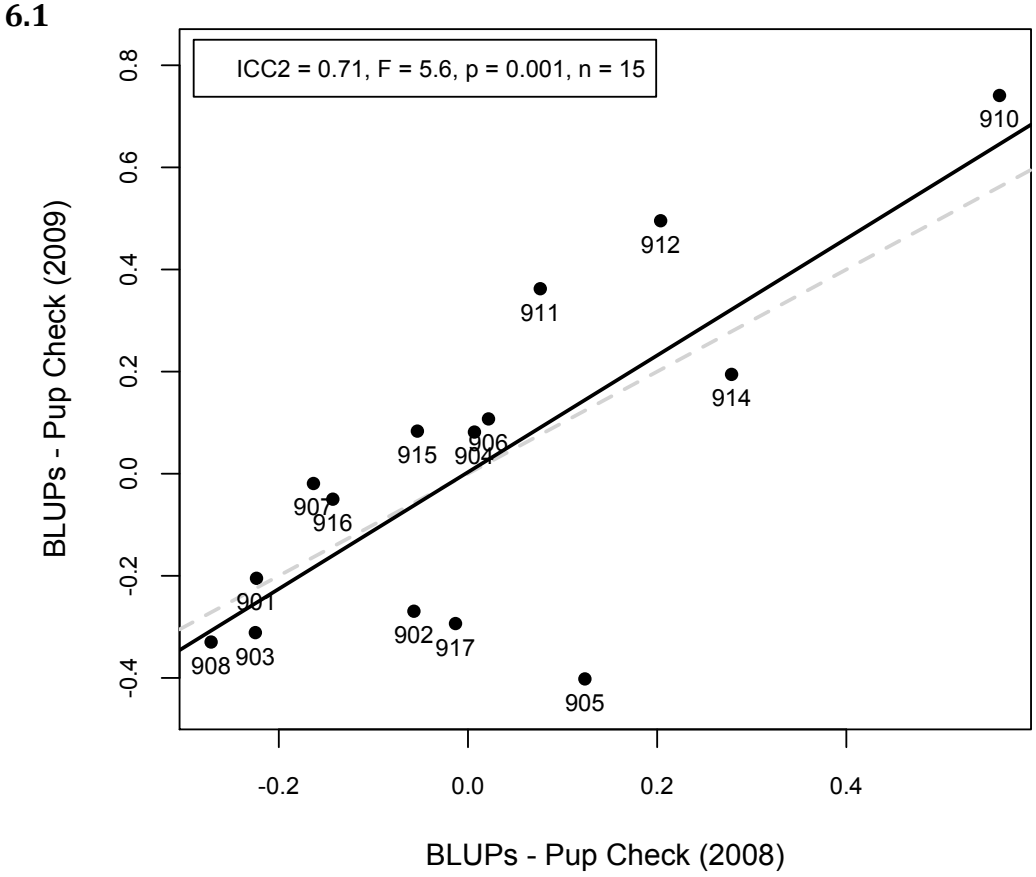
Table 6.3: ICC2 analyses for the BLUPs extracted from the simplest models for the individuals re-sighted in all 3 years (n = 8), 2007 & 2008 (n = 9), 2008 & 2009 (n = 15), 2007 & 2009 (n = 9) for the pup check and alert behavioural categories. All significant results are in bold. The simplest models for the pup check and alert behaviours are shown in bold in Tables 6.1 and 6.2, respectively. The lower and upper columns show the 95% confidence limits.

Behaviour	Years	ICC	F	*p*	lower	upper
Pup	2007 - 2009	0.03	1.1	0.42	-0.35	0.6
Check	2007 & 2008	0.009	1	0.49	-0.76	0.66
	2008 & 2009	**0.71**	**5.6**	**0.001**	**0.31**	**0.89**
	2007 & 2009	0.12	1.3	0.37	-0.67	0.72
Alert	**2007 - 2009**	**0.62**	**5.3**	**0.004**	**0.18**	**0.9**
	2007 & 2008	**0.65**	**4.3**	**0.027**	**-0.015**	**0.91**
	2008 & 2009	**0.68**	**5**	**0.002**	**0.27**	**0.88**
	2007 & 2009	**0.66**	**4.5**	**0.025**	**0.004**	**0.91**

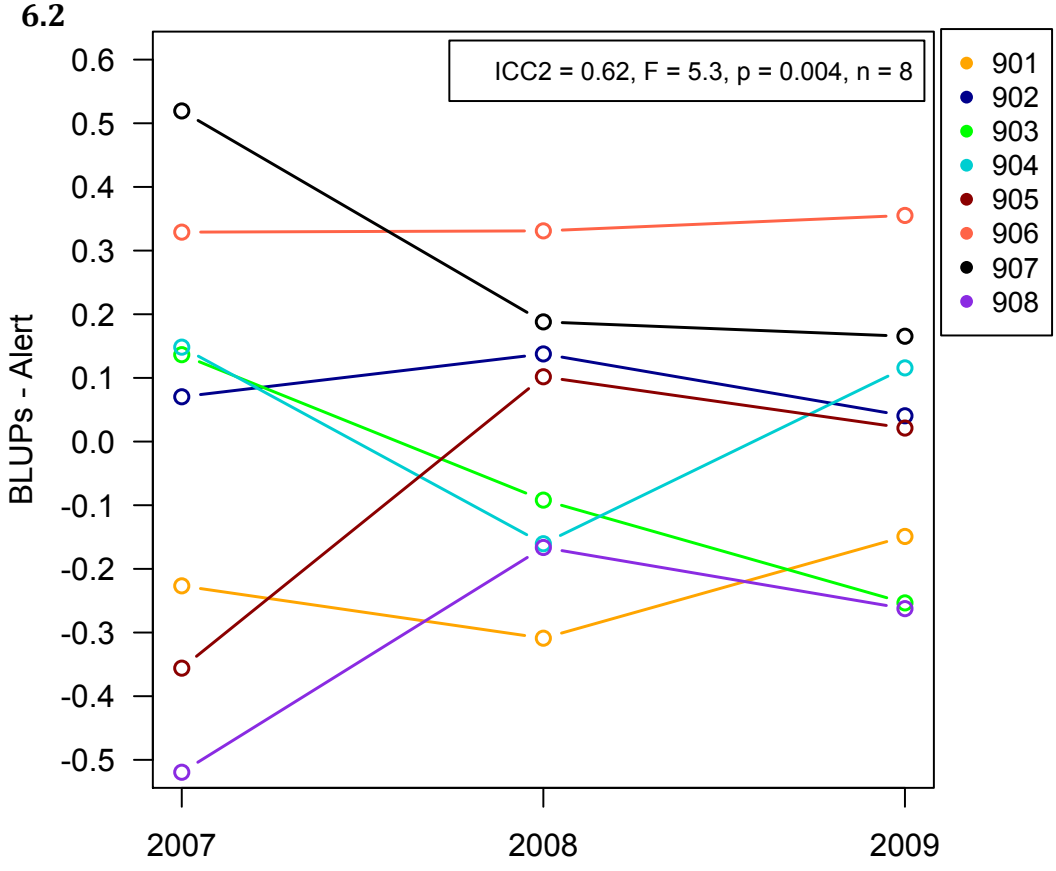
The following 3 pages show:

Figure 6.1 - 6.5: The plots of the significant repeatability estimates for the BLUPs extracted from the simplest models for the: **6.1)**. Pup check (2008 & 2009) and, **6.2, 6.3, 6.4, 6.5)**. Alert (2007 - 2009; 2007 & 2008; 2008 & 2009; 2007 & 2009, respectively) behavioural categories. ICC2 results are shown in the legend within each of the plots. For the figures presenting three years of data the individual ID numbers are shown in the legend out-with the plot and are colour coded to the plotted lines. For the figures presenting two years of data the individual ID numbers are given for each data point. The line of best fit (black solid line) and the 1:1 line (grey dashed line) are presented in the pairwise plots. The simplest models for the pup check and alert behaviours are shown in bold in Tables 6.1 and 6.2, respectively.

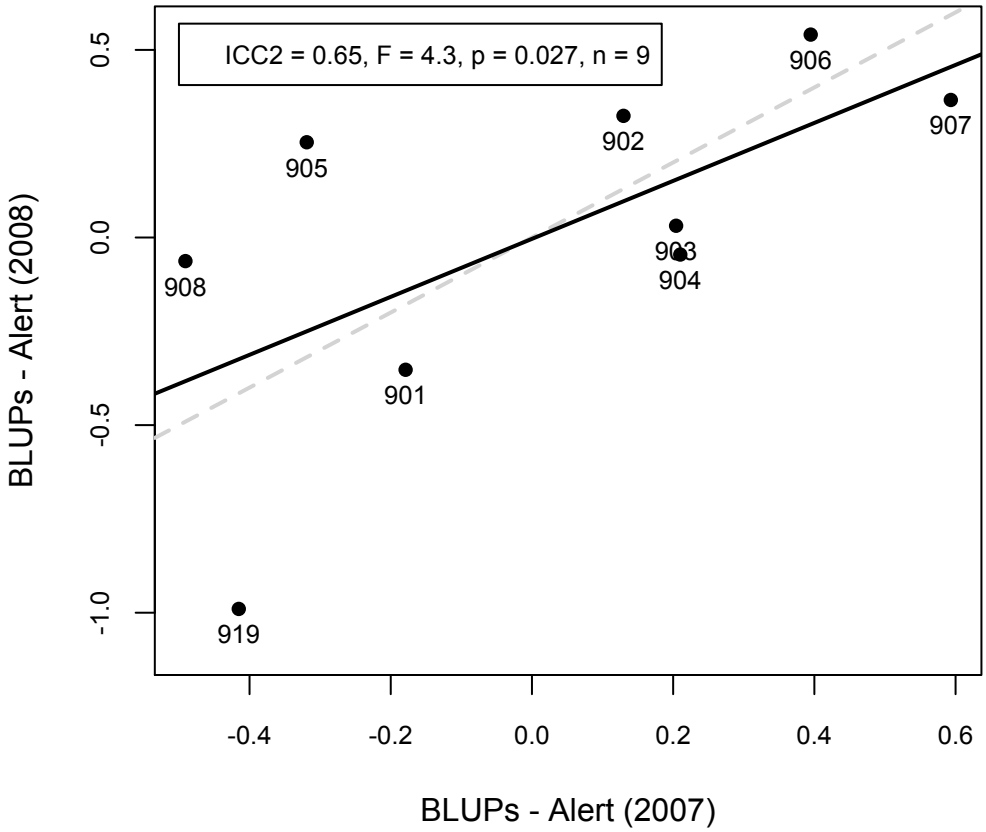
6.1


ICC2 = 0.71, F = 5.6, p = 0.001, n = 15
BLUPs - Pup Check (2009)
BLUPs - Pup Check (2008)
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.2
0.0
0.2
0.4
910
912
911
914
915
906
904
907
916
901
902
917
908
903
905

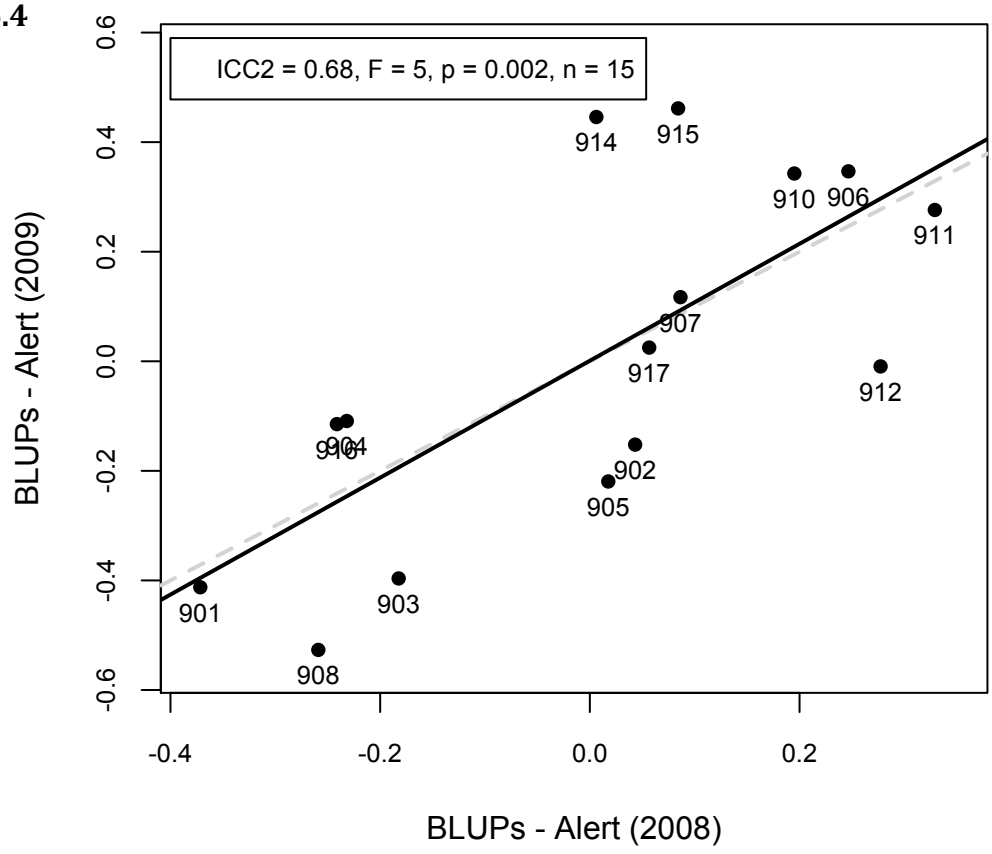
6.2


ICC2 = 0.62, F = 5.3, p = 0.004, n = 8
BLUPs - Alert
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
2007
2008
2009
901
902
903
904
905
906
907
908

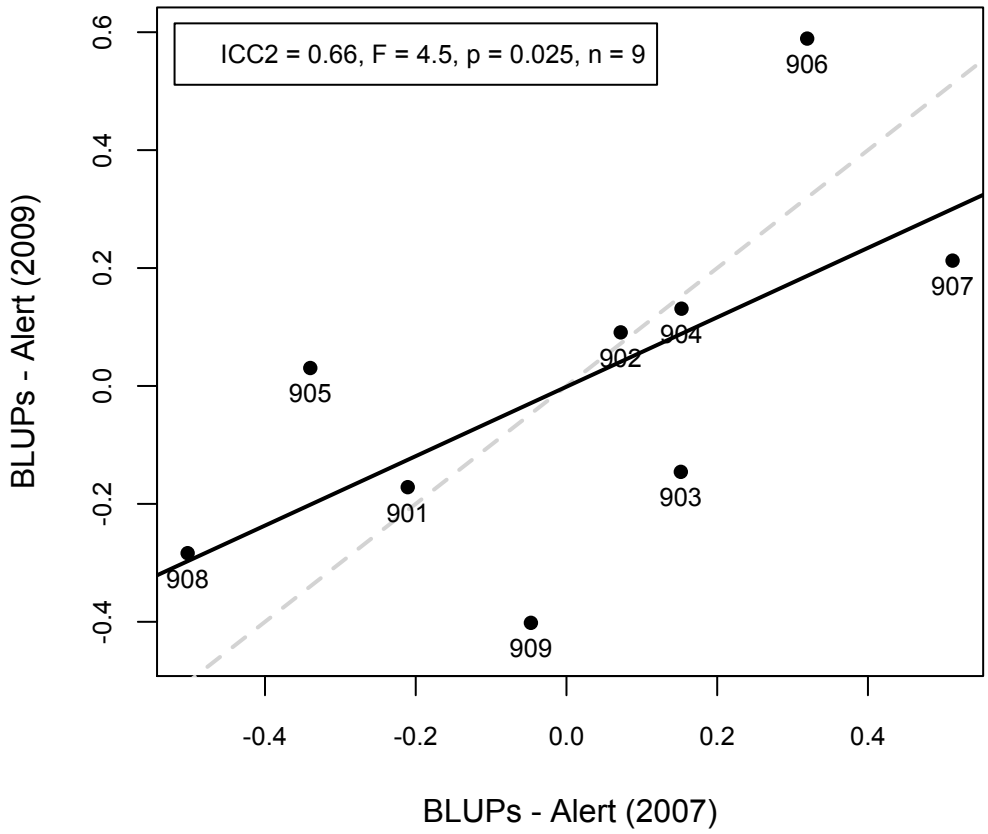
6.3


ICC2 = 0.65, F = 4.3, p = 0.027, n = 9
BLUPs - Alert (2008)
BLUPs - Alert (2007)
0.5
0.0
-0.5
-1.0
-0.4
-0.2
0.0
0.2
0.4
0.6
906
907
902
905
903
904
908
901
919

6.4


ICC2 = 0.68, F = 5, p = 0.002, n = 15
BLUPs - Alert (2009)
BLUPs - Alert (2008)
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.4
-0.2
0.0
0.2
914
915
910
906
911
907
917
912
902
905
901
903
908

6.5



6.6. Discussion

Following the approach used in Chapter 5, Section 5.5, the initial sections below shall provide a biological interpretation of the models retained within the confidence sets for each of the behavioural categories. Subsequently, the results from the present chapter shall be compared to those in Chapters 4 and 5, prior to discussing the caveats and limitations to GLMMs with respect to these data.

6.6.1. Pup check

For the pup check behavioural category, the variance explained by individuals' ID ranged from < 0.001 to 0.381. Therefore, for some models, the majority of the variance in the pup check behaviour was explained by the fixed effects. The most influential fixed effect (irrespective of breeding season or the group of re-sighted individuals) was the activity of the pup, which had a positive

relationship with the pup checking behaviour. In 2009, the distance to the nearest pool was also influential, and was retained in all of the 'best' models. It too had a positive relationship; however, as noted in Chapter 5, Section 5.5.1, this covariate also has a significant, negative relationship with the distance between the mother and her pup (Chapter 3, Section 3.14). Therefore, in 2009, the closer a mother was to her pup, the more time she spent pup checking, which although somewhat confounding, does make biological sense. Given that both of these patterns were also identified in the GLMs, the same biological interpretation of these findings applies here, and shall not be reiterated (see Chapter 5, Section 5.5.1).

In addition to these findings, the variance explained by individuals' ID in all of the 2007 datasets was comparably higher than that of the 2008 and 2009 datasets. A similar pattern was also identified in Chapter 5, Section 5.4.2, where individuals' ID was retained in all of the 'best' GLMs for the 2007 datasets. This increase in individual variation may be explained by the extreme environmental conditions that occurred during the first three weeks of the 2007 breeding season, when it was relatively warm and atypically dry (Chapter 3, Section 3.14). Such conditions are known to result in mothers spending longer periods of time apart from their pups, because they have to commute longer distances to pools of water (Redman et al., 2001). Despite this general pattern shown by Redman et al. (2001), such extreme conditions are likely to result in extreme variation in behaviour, as females attempt to balance the potential costs of reproductive failure (increased probability of permanent separation from their pup; Anderson et al., 1979; Baker, 1988; Baker & Baker, 1988) and the need to gain access to water for thermoregulation and/or to maintain a positive water balance (Twiss et al., 2000; Redman et al., 2001; Twiss et al., 2001). Therefore, this fundamentally important life-history trade-off, coupled with the extreme environmental conditions, may account for the greater variance explained by individuals' ID in the 2007 datasets (e.g. Nussey et al., 2005b; Nussey et al., 2007b).

Once the fixed-effect covariates were accounted for, the pup checking behaviour was found to be repeatable for the individuals that were re-sighted in 2008 & 2009, only. The repeatability estimates obtained using the gross activity budget data yielded the same outcome (Chapter 4), and both sets of repeatability

estimates (from the hourly activity budgets and from the gross activity budgets) are supported by the GLMs presented in Chapter 5. Consequently, the biological interpretation for this behaviour remains unaltered from Chapter 5 (Section 5.5.1); the pup check behaviour is heavily influenced (either directly or indirectly) by the behaviour of the pup. As a result, the majority of the variance is typically explained by the relevant fixed-effects (e.g. pup activity and distance to pup), as opposed to the individuals' ID. Where repeatability did occur, sample sizes were larger, and the increased variance was dependent on one or two individuals. Therefore, in order to identify repeatability in the pup check behaviour, it may be that larger sample sizes are required. Furthermore, the data suggest that under extreme environmental stress, repeatability in the pup check behaviour may 'disappear' as individuals are forced to balance an important trade-off between time spent with their pup and time spent commuting to and from pools of water (Redman et al., 2001). Therefore, identifying repeatability of the pup check behaviour may also be dependent on the environmental conditions experienced by the group of individuals.

6.6.2. Alert

For the alert behavioural category, the variance explained by individuals' ID ranged from 0.054 to 0.225. Therefore, in all models, individuals' ID did explain some of the variance in the alert behaviour. The most influential fixed effect (irrespective of breeding season or the group of re-sighted individuals') was the activity of the pup, which had a positive relationship with the alert behaviour. As was stated in the previous section, mothers are known to respond to their pup's behaviour (Fogdon, 1971; Kovacs, 1987; Smiseth & Lorentsen, 1995a, b; Smiseth & Lorentsen, 2001; Chapter 3, Section 3.14); therefore, this finding is unsurprising. For the 2008 breeding season, the models showed that lower levels of rainfall or being closer to a female neighbour, resulted in a higher proportion of time spent alert. However, for the 2008 datasets, both of these covariates had a significant, positive relationship with one another, and they were also correlated with density (negative relationship) and the distance to the nearest pool (positive relationship). Therefore, in a 'typical' breeding season (with respects to the environmental conditions; Chapter 3, Section 3.14), it is likely that females were more alert the

closer they were to pools of water, which were in higher density areas. Conversely, females were less alert when rainfall increased, because their need to commute to pools of water was reduced, which meant that they could remain closer to their pups (which were typically in lower density areas).

In the 2007 breeding season, the models found that the converse relationship occurred; the further a female was from a pool of water, the more alert she was. However, in 2007, this covariate was negatively collinear with distance to pup, density and air temperature, and was also positively collinear with the distance to the nearest female neighbour and pup age (Chapter 3, Section 3.14). Therefore, there were a number of possible covariates influencing the alert behaviour during the 2007 breeding season, and as a result, it is unlikely that there was a straightforward relationship between this behaviour and a single covariate. It is however, more likely that the trade-off between the distance to the pool and the distance to the pup was the more influential (Twiss et al., 2000; Redman et al., 2001; Chapter 3, Section 3.14); although, as was inferred in the 2008 models, one would expect that the closer females were to pools (which are typically areas of higher density), the more alert they would be. The counterintuitive positive relationship between distance to the nearest pool and the alert behaviour in 2007 may be explained by the atypically dry and relatively warm conditions, which were shown to interfere with otherwise strongly significant relationships between covariates in the 2008 and 2009 breeding seasons (Chapter 3, Section 3.14). Similar to the findings for the pup check behavioural category, these extreme environmental conditions may have resulted in extreme variations in behaviour, which (even with such fine-scale data) are not straightforward to interpret.

Nevertheless, once the influence of these fixed effects was accounted for, the alert behaviour was found to be highly repeatable across all four groups of re-sighted individuals. Furthermore, with the exception of the individuals re-sighted in 2007 & 2009, the repeatability estimates were robust to all possible model combinations. The exception to the trend may be due to the longer time period between re-sampling, which has been shown to reduce repeatability estimates (Bell et al., 2009) and/or it may be due to the contrasting environmental conditions between the two breeding seasons (atypically dry and warm compared to

atypically wet and cold, Chapter 3, Section 3.14). Nevertheless, the repeatability estimates from the simplest models yielded the same outcome as the repeatability estimates obtained using the gross activity budget data (Chapter 4), and both sets of repeatability estimates (from the hourly activity budgets and from the gross activity budgets) are supported by the GLMs presented in Chapter 5.

In summary, the GLMMs (and the GLMs; Chapter 5, Sections 5.4.3 and 5.5.2) showed that the variance in the alert behaviour was explained by a combination of the individuals' ID, the activity of the pup and several spatial and environmental covariates that varied between breeding seasons. However, despite the influence of the fixed effects, the variance explained by individuals' ID was consistent. Therefore, the repeatability estimates for the alert behaviour of wild, postpartum female grey seals were both highly significant and highly robust. The potential ecological and evolutionary reasons for why this may be shall be discussed in Chapter 9.

6.6.3. Suitability of GLMMs to these data

As expected, the binomial distribution fitted the pup check data well and there was no discernable evidence to suggest that overdispersion was an issue. Therefore, there are no concerns with respects to applying a GLMM with a binomial distribution to these data. Conversely, for the alert behaviour, the binomial distribution fitted the data reasonably well for observed occurrences ≤ 1, but where the observed occurrences were > 1, the model typically failed to predict these data. It is acknowledged that overdispersion (the occurrence of more variance in the data than predicted by the model; Bolker et al., 2009) can lead to selecting overly complex models, which can lead to poor ecological inference (Hinde & Demétrio, 1998; Burnham & Anderson, 2002; Richards, 2008). However, the estimated dispersion was not considerably greater than 1 for any of the alert models (ranged between 1.121 - 1.463). Furthermore, the confidence sets for the GLMMs were very similar to the confidence sets for the GLMs. Therefore, although the beta-binomial was the preferred distribution, using the binomial distribution did not result in selecting overly complex models (as supported by the GLMs using a beta-binomial distribution).

6.6.4. The use of BLUPs to answer ecological questions

The opinions on the use of BLUPs in ecology and evolutionary biology have changed recently. Several of the authors that have pioneered the use of BLUPs to answer questions in these fields (e.g. Kruuk, 2004; Nussey et al., 2005a; Martin & Réale, 2008a, b) are now discouraging the use of BLUPs as an inferential tool in ecological and evolutionary biology (Hadfield et al., 2010; Morrissey et al., 2010; Wilson et al., 2010). In a recent publication, Hadfield et al. (2010) discussed three principal criticisms on the misuse of BLUPs, and they do this in the context of the intended purpose of BLUPs (which is to predict the expected phenotype of an animal's offspring using an individual's breeding value; Robinson, 1991). Their concerns and criticisms are: 1) BLUP is an unbiased predictor of breeding value only when the model used to make the predictions is the correct one, 2) the properties of BLUPs hold only for the context of predicting the mean of a single breeding value and that these properties do not extend to other aspects of an individual's breeding value and do not extend to higher-level statistics summarising the distribution of breeding values in a population, 3) the large amount of prediction error and complicated patterns of dependence in predicted breeding values are usually not accounted for when quantifying uncertainty, and this can lead to extreme anticonservatism.

The first of these criticisms is of course true of any model. Given that the true best model is unlikely to be known, one can only follow the guidelines and protocols to ensure that the analytical approaches used are the most suitable for the data being analysed and the questions being addressed. Furthermore, in the present study the hypotheses were built on a wealth of knowledge from previous studies, which meant that data were collected and modelled with a firm understanding of the factors that influence grey seal behaviour whilst on the breeding colony.

With respect to the present study, the second criticism does not seem applicable given that the BLUPs were not used in 'higher-level statistics' to make inference on 'other' aspects of the individual's and/or population's ecology. In

comparison, many ecological studies that have extracted BLUPs from GLMMs go on to include the BLUPs as a measure of the random effect (e.g. a measure of the individuals' behaviour or fitness) in further analyses (typically principal component analyses (PCA)). Several studies have used this approach to address questions on specific behavioural traits in relation to environmental sensitivity (Minderman et al., 2009), habitat choice (Boon et al., 2008), habituation (Martin & Réale, 2008a) offspring fitness (Boon et al., 2007) and individual quality (Moyes et al., 2009). Therefore, the approach used in the present study is somewhat analytically simplistic in comparison, and does not 'manipulate' the BLUPs in any way.

The third criticism is based on the fact that the variance values of BLUPs are consistently less than the variance of the true values (Hadfield et al., 2010). This in part relates to the previous point, because the BLUPs are not used in 'higher-level statistics', and given that it is the BLUPs themselves that are being compared directly; then ignoring the reduced variance may not be as important in this instance (compared to making inference on BLUPs that have been used to form a principal component axis in a PCA). Therefore, the concerns regarding the misuse of BLUPs that have been raised by Hadfield et al. (2010) and echoed by Wilson et al. (2010) are not applicable in the case of the present study. Nevertheless, it was deemed important to address these issues, as an increasing number of researchers are raising them (Hadfield et al., 2010; Morrissey et al., 2010; Wilson et al., 2010).

6.7. Conclusions

The analytical approaches developed in this chapter and the previous two chapters, have shown that it is possible to use 'hands-off' observational data to identify CIDs in the behaviour of wild postpartum female grey seals in the field. This approach has been developed so that each step reinforces the findings in the subsequent step, which was deemed to be particularly important when the assumptions and/or limitations to the analytical techniques could not always be fully met. Therefore, this thesis has developed a novel three-step analytical process for identifying CIDs in behaviour by using: 1) the ICC to identify repeatability in the gross data, 2) the GLMs to identify the importance of

individuals' ID whilst considering the influence of other covariates, 3) the GLMMs to quantify the repeatability in behaviour, despite the influence of other covariates. However, it is fundamentally important that this three-step analytical process is applied to other empirical datasets to assess how robust it is to deviations from the observational approach used in the present study.

Chapter Seven:
The application of the three-step analytical process for identifying consistent individual differences in behaviour

7.1. Introduction

Over the course of the previous three chapters, a three-step analytical process was developed to ascertain whether or not consistent individual differences (CIDs) in behaviour did occur within groups of wild, postpartum female grey seals. The results from this completely observational, 'hands-off' study showed that CIDs in the alert behavioural category and, to some extent, the pup check behavioural category did occur, despite accounting for the effect of other influential covariates. However, prior to suggesting the optimum approach for identifying CIDs in behaviour by using this novel approach, it is fundamentally important to assess how robust this analytical process is to deviations from the data collection procedures used in the north study area (NSA).

7.2. Aims

This chapter will apply the three-step analytical approach to an independent dataset collected on postpartum female grey seals that were present in the study area (SA) of North Rona (Chapter 2, Section 2.3) during the 2008, 2009 and 2010 breeding seasons. The principal aim of these analyses is to assess whether or not deviations from the sampling protocol used in the NSA reduced the likelihood of identifying CIDs in behaviour where, based on previous research (Twiss & Franklin, 2010; Twiss et al., 2011a) and the results presented in the previous three chapters, one would expect them to occur. The results from the SA and the NSA shall be compared, and the influence of the variation between the sampling protocols (with respect to how robust the three-step analytical process is), shall be discussed.

7.3. Methods

7.3.1. Data collection in the SA

The SA covers an area of approximately 0.38 km^2. A few narrow gullies on the east side of the island give seals access from the sea to an open, boulder-strewn grassy slope (Chapter 2, Section 2.3; Pomeroy et al., 2005). During the 2008, 2009 and 2010 breeding seasons, Dr. Sean Twiss (SDT) collected behavioural observations in the SA from a hide on a ridge that was approximately 40 m higher than the SA (Twiss, 1991). From this vantage point, the distance between SDT and target individuals ranged between approximately 100 m to 500 m. SDT used the same ethogram as was used in the NSA by Ross Culloch (RMC) and both SDT and RMC used 5 minute scan samples (Chapter 2, Section 2.5.4). Due to other fieldwork commitments, SDT could not carry out behavioural observations all day, every day. Consequently, behavioural observations on each of the known individuals were intermittent throughout their lactation (Tables A7.1 - A7.3). This intermittent approach to gathering behavioural data generally resulted in a smaller number of scan samples per individual (as compared to the NSA), particularly for the early and late lactation periods (Chapter 3, Section 3.6). Consequently, all available data, postpartum, were used in all of the analyses (irrespective of lactation period; Chapter 4, Section 4.5.1).

7.3.2. The gross activity budget and the gross spatial data

The exploratory analyses of the NSA data suggested that ≥ 200 scan samples are required in order to obtain an accurate representation of a postpartum female grey seal's activity (Chapter 3, Section 3.4; Figure A7.1). By applying this cut-off to the SA data, 11 individuals were omitted from the gross dataset. There were a further 10 individuals omitted because: three had a dead pup, three adopted a pup, two were out-of-sight for a large proportion of time (≥ 0.5), two were in awkward locations (down steep gullies) and were often partially out-of-sight, which made behavioural observations difficult (Figure A7.1). The gross activity budget of the remaining 70 individuals is presented in Table A7.4.

Of the individuals included in the behavioural observations, the majority were also included in the ongoing, long-term studies on North Rona (Chapter 2, Section 2.3.1). Therefore, the majority of these females and their pups were caught and handled twice during lactation, once in the early stages and once in the later stages (for a detailed description of the methods used to capture and handle mothers and their pups, see Pomeroy et al., 1999). The long-term studies also include mapping all of the seals within the SA once a day. Mapping in 2008 - 2010 was done by Dr. Paddy Pomeroy (PPP), and was typically done between 08:00 and 12:00. The principal aim of these maps was to record the location of seals, their sex and age class (e.g. male, female, pup, weaner, juvenile) and to identify the location of known females.

The time taken to map the SA was kept to a minimum so that the locations of the seals relative to one another were as accurate as possible. Consequently, in the time given to map the SA it was not always possible to identify which pup belonged to which mother; therefore, the identity of the pup was not always recorded on these daily maps. As a result, it was not possible to extract the mother-pup distances for the known individuals in the SA. However, given that the exploratory analyses of the NSA data showed that the distance between the mother and her pup, and the distance between a mother and her nearest pool had a strongly significant, negative relationship (Chapter 3, Section 3.14), it was assumed that the same pattern was also true for the SA. Therefore, for the SA data, the distance to the nearest pool will also be used as a proxy for the distance between a mother and her pup. For all three breeding seasons, the distance between a female and her nearest pool was calculated using a pool coverage from the 1994 breeding season (which was the most recent coverage available; see Chapter 2, Sections 2.5.5 and 2.5.6 for more information on how the coverage was created and how the data were extracted from the GIS database).

It was not possible to include home range usage in the analyses of the SA data, because the minimum number of locations required to accurately calculate the kernel density estimate (KDE) is 30 (Seaman et al., 1999; Chapter 2, Section 2.5.6). Even if PPP positively identified a known individual every day postpartum, this would only have given approximately 18 to 20 locations (Pomeroy et al.,

1999). Therefore, to prevent making inference on poor estimates of home range, the KDEs for the SA data were not included in the subsequent analyses. As a consequence, it was not possible to calculate the site fidelity measure for the distance between the centre of the core area of an individual's home range between breeding seasons (Chapter 3, Section 3.10). Nevertheless, it was possible to calculate the pupping site fidelity (Chapter 3, Section 3.10); however, these data showed that a high proportion of the re-sighted females' pups were more than 3 days old (stage 2 pups or older; Chapter 2, Section 2.5.8) by the time of the first map (which was the location used to define the pupping site location; Tables A7.5 and A7.6). Given that the first few days postpartum appear to be important with respect to home range usage (Chapter 3, Section 3.8.2), it is less likely that a mother's location after 3 days postpartum reflects the location of her pupping site. Therefore, the pupping site fidelity will not be considered in any of the subsequent analyses. Of the 70 individuals included in the gross activity budget, 6 did not have any associated spatial data. The summary data for the 64 individuals for the three spatial covariates are shown in Table A7.7.

7.3.3. Data structure

Throughout the three-step analytical process (Section 7.3.4, below), the SA data were analysed in the same manner as the NSA data. Therefore, step 1 used one data point taken from the gross activity budget for each individual, for each breeding season (Chapter 4, Section 4.5). Steps 2 and 3 used hourly activity budgets, which meant that there were multiple data points for each individual, for each breeding season (Chapter 3, Section 3.11). The datasets for all three steps are referred to as re-sighted individuals' datasets, of which, there were nine (i.e. 2008 - 2010 = 3; 2008 & 2009 = 2; 2009 & 2010 = 2; 2008 & 2010 = 2). The SA behavioural data were divided into the same eight behavioural categories that were used for the NSA (Chapter 2, Section 2.5.3). All eight of these behavioural categories were included in step 1; however, based on the results of the NSA data, only the pup check and alert behavioural categories shall included in steps 2 and 3 of the analyses.

7.3.4. The three-step analytical process

Over the previous three chapters, a novel three-step analytical process for identifying CIDs in the behaviour of wild postpartum grey seals was developed. The rationale and the approach for applying this process is briefly summarised below:

1. The first step uses the gross activity budget to identify whether or not repeatability in behaviour occurs across breeding seasons, irrespective of potentially influential extrinsic and/or intrinsic covariates. This is done using the intraclass correlation coefficient (ICC). This step gives an initial indication as to which, if any, of the behaviours are repeatable (see Chapter 4 for more information on step 1);

2. The second step uses a suitable fixed-effects model to analyse each of the re-sighted individuals' datasets. The individuals' unique identification code (individuals' ID) is included in these models as a fixed effect along with the other available covariates that are known, or are suspected to, influence the behaviour of interest. This analysis identifies which covariates (including individuals' ID) best explain the variation in behaviour within a breeding season (see Chapter 5 for more information on step 2);

3. The third step uses a suitable mixed-effects model to analyse each of the re-sighted individuals' datasets. Individuals' ID is included as a random effect whilst the other covariates (that were included in the model in step 2) are included as fixed effects. The best linear unbiased predictors (BLUPs), which provide estimates of the random effects (individuals' ID) independent of the other terms within the model, are extracted from all of the models retained within the confidence sets. Using the ICC, the repeatability of the BLUPs for the four groups of re-sighted individuals shall be estimated across the relevant confidence sets. Furthermore, to assess how robust these repeatability estimates are, the BLUPs of re-sighted individuals shall be compared across all combinations of the models retained within the confidence sets. Therefore, step 3 tests for CIDs in behaviour

once the influential covariates that are retained within the mixed-effects model are accounted for (see Chapter 6 for more information on step 3).

7.3.5. The comparative analyses between the SA and NSA datasets

Quantitative comparisons of the behavioural and spatial data between the two study sites were carried out separately, for the 2008 and 2009 breeding seasons. This approach was preferred to comparing the three years of data collectively for each of the study areas because environmental covariates, such as rainfall and air temperature, which are known to influence behaviour (Twiss et al., 2000; Redman et al., 2001; Twiss et al., 2002), varied considerably between breeding seasons (Chapter 3, Section 3.14). The comparative analyses of the gross activity budgets showed that there was no significant difference between the pup check, alert or pup interactions behavioural categories between the two study sites in 2008 or 2009 (Table A7.8 and Figure 7.1). However, in the SA, in at least one of the two breeding seasons, individuals did spend significantly more time in the resting, locomotion and presenting & nursing behavioural categories, and significantly less time in the comfort movement and aggression behavioural categories. With respect to the spatial data, density was not significantly different in either breeding season, whereas the female's in the NSA were significantly closer to their nearest female neighbour in 2008, and the female's in the SA were significantly closer to their nearest pool in 2009 (Table A7.9 and Figure 7.2). The potential reasons for these significant differences in the behavioural and spatial data between the SA and the NSA are discussed in Section A of the Appendix.

The repeatability of all eight behavioural categories shall be estimated in step 1, irrespective of the significant differences between the two study sites for some of the behavioural categories. However, based on the findings of previous studies (Twiss & Franklin, 2010; Twiss et al., 2011a) and the results presented in Chapters 4, 5 and 6, only the plots of the significant repeatability estimates for the pup check and the alert behavioural categories shall be presented in the main part of this chapter. Furthermore, as the gross activity budgets for these behavioural categories were not significantly different between the two study sites, it is possible to make direct comparisons between the results from the SA and the

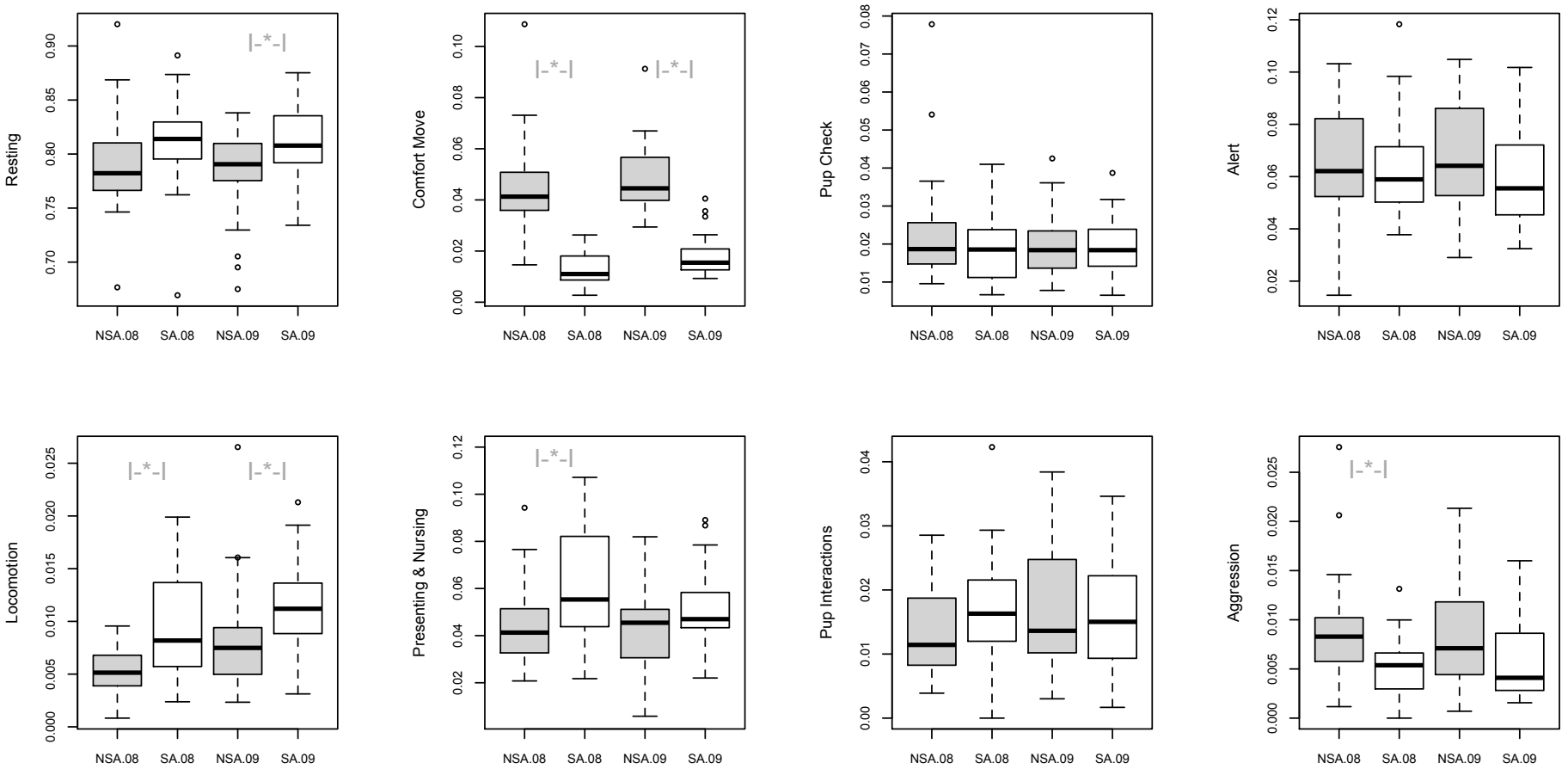


Figure 7.1: The proportion of time that postpartum females from the north study area (NSA) (n = 28, 2008; n = 30, 2009) and the study area (SA) (n = 20, 2008; n = 23, 2009) spent in each of the eight behavioural categories during the 2008 (.08) and 2009 (.09) breeding seasons. The behavioural categories are shown on the y-axis. See table A7.8 for the results of the statistical analyses comparing these data. Significant results are indicated by the |-*-| symbol.

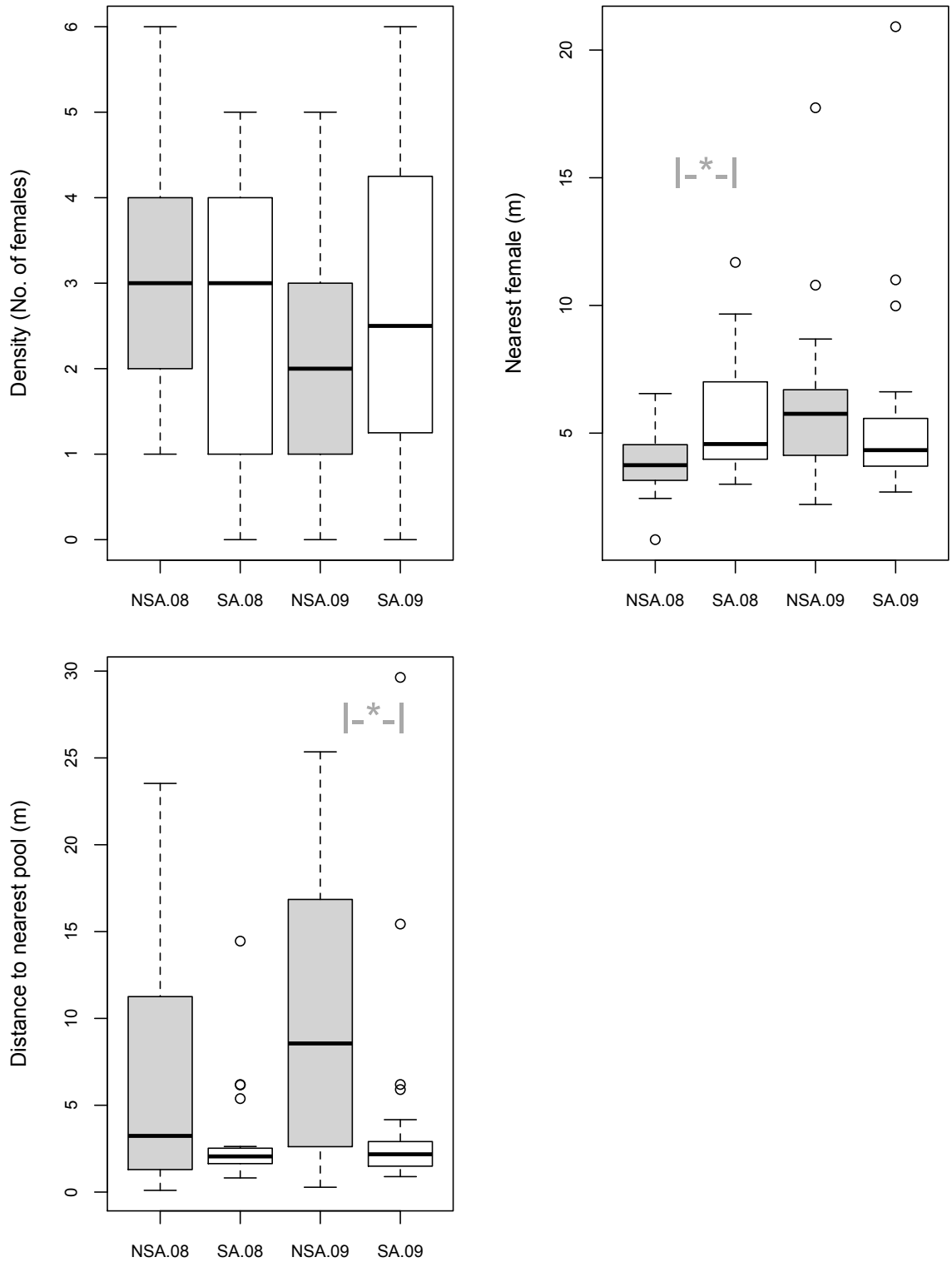


Figure 7.2: The comparisons between the spatial covariates for the postpartum females in the NSA (n = 28, 2008; n = 30, 2009) and the SA (n = 20, 2008; n = 23, 2009) during the 2008 (.08) and 2009 (.09) breeding seasons. The spatial covariate being compared is labelled on the y-axis. See table A7.9 for the results of the statistical analyses comparing these data. Significant results are indicated by the |-*-| symbol.

NSA analyses. The plots of the significant repeatability estimates for the other behavioural categories shall be presented in the Appendix, as they are not behaviours of principal interest.

7.3.6. Re-sighted individuals

Of the re-sighted individuals included in the SA analyses, there were 5 known individuals re-sighted in all three years, 9 additional known individuals that were re-sighted in two consecutive years and 4 known individuals that were re-sighted in non-consecutive years (no data collected, or individual not present during the 2009 breeding season). Therefore there were a total of 18 *actual* individuals (N = 18; which account for a total of 41 individuals over the three breeding seasons, n = 41). Each of the individuals (N = 18) that were re-sighted in the SA were given a prefix of '99', followed by a number starting at '1'; these unique individual ID codes shall be used in the relevant tables and figures throughout this chapter.

7.3.7. Covariates included in the analyses

The covariates that were used in steps 2 and 3 of the analyses were the: 1) distance between a female and her nearest pool (m), 2) distance between a female and her nearest female neighbour (m), 3) density of females around the target female (using a 10 m buffer zone), 4) pup age (days postpartum), 5) air temperature (^{o}C), 6) proportion of time the females' pup spent active, 7) individuals' unique identification code (Individuals' ID) (see Chapter 3, Section 3.14 and Chapter 5, Section 5.3.4 for the rationale for including these covariates in the analyses). Covariates 1 - 4 were recorded daily and covariates 5 and 6 were recorded hourly. The air temperature data were derived from the same datasets that were used in the NSA analyses (see Chapter 2, Section 2.5.7 for more details on how the data for this covariate was collected and derived). Pup activity was calculated using the same method as described in Chapter 3, Section 3.11. There was a significant difference between the proportion of time pups spent active across the groups of data, based on the total number of scan samples collected per hour (ANOVA, $F_{(1,3335)} = 252.19$; $p < 0.001$; Figure A7.2). However, there is no

clear pattern to suggest that the proportion of time spent active decreases with sample size, for example. To be thoroughly confident that no such pattern exists in these data, the same plot was reproduced for each of the re-sighted females' pups, for each of the breeding seasons (plots are not presented). Similarly, none of these plots showed any pattern to suggest that there was a relationship between the number of scan samples collected per hour, and the proportion of time the pup spent active.

During the 2010 breeding season, no rainfall data were collected; however, this covariate was consistently collinear with air temperature across all of the re-sighted individuals' datasets for 2008 and 2009 (see Appendix, Section A, Tables A7.10, A7.11, A7.13 - A7.15, A7.17). Therefore, it was decided to omit rainfall from the subsequent analyses. Consequently, by including the same covariates within each of the global models, it was possible to directly compare models both within and between the three breeding seasons. A complete account of the collinearity analyses of the SA data is presented in Section A of the Appendix (Tables A7.10 - A7.18). In summary, these analyses showed that there was a lot of variability and inconsistency in the collinearity of the explanatory variables. Consequently, it was decided to include all covariates (with the exception of rainfall) in the subsequent analyses, which means that collinearity of covariates did occur in each of the nine re-sighted individuals' datasets. This issue shall be addressed during the model selection process (see Section 7.3.8, below).

7.3.8. Model selection, model inference and goodness-of-fit

Following the methods used in Chapter 3, Section 3.12, the exploratory analyses of the pup check and the alert behavioural categories showed that there was no evidence of temporal autocorrelation in any of the re-sighted individuals' datasets at the individual- or population-level (plots not presented). To test for zero-inflation, the approach detailed in Chapter 3, Section 3.13, was followed. For the majority of the models for both behavioural categories, the beta-binomial distribution fitted the data best (Tables A7.19 and A7.20). Therefore, to maintain consistency in the analyses, a generalised linear model (GLM) with a beta-binomial distribution and a logit link was used in step 2 of the analyses for all re-

sighted individuals' datasets, for both behavioural categories (See Chapter 5, Section 5.3 for further rationale on this approach).

Model selection was carried out using AICc (see Chapter 5, Appendix, Section B) and the five-step process for model selection (Chapter 5, Section 5.3.6) was used to define the confidence sets. The approach used for model inference and assessing goodness-of-fit as presented in Chapter 5, Sections 5.3.7 and 5.3.8 was followed. Using the simplest model with the lowest AICc, the response variable was predicted for continuous covariates that had an estimate greater than twice the standard error. In order to do this, the covariate of interest was allowed to vary within its observed range whilst the other covariates retained within the simplest model were standardised to their mean (Crawley, 2007). For the observed values, the continuous covariates were binned at standard intervals. The response variable was also predicted for individuals' ID (categorical covariate) if it was retained within the model (see Chapter 5, Section 5.3.8 for more information). To avoid presenting multiple plots, inference shall be made for each year using models that best illustrated the general trends found throughout the data and maximise the sample sizes (number of scan samples and number of re-sighted individuals).

A generalised linear mixed model (GLMM) with a binomial distribution and a logit link was used in step 3 of the analyses (as it is not possible to model non-normal, overdispersed data using the *lme4* package; Chapter 6, Section 6.4.4). Based on the findings above (Tables A7.19 and A7.20) the GLMMs were expected to be overdispersed; however, the exploratory analyses showed that overdispersion for the pup check and alert behavioural categories was most probably negligible (ranging between 0.969 - 1.234 and 1.140 - 1.334, respectively; Table A7.21). Nevertheless, it is acknowledged that using the binomial distribution with overdispersed datasets could lead to serious problems (Hinde & Demetrio, 1998; Richards, 2008), which were discussed in Chapter 6, Sections 6.4.4 and 6.6.3. Model selection was carried out using AIC (as it is not possible to calculate AICc for GLMMs; Chapter 6, Section 6.4.2). The five-step process for model selection (Chapter 5, Section 5.3.6) was used to define the confidence sets and goodness-of-fit was assessed using the simplest model with

the lowest AIC (Chapter 5, Section 5.3.8). Only data that yielded significant repeatability estimates were plotted (using the simplest models with the lowest AIC).

7.4. Results

7.4.1. Step 1: Repeatability of the gross activity budgets

Repeatability occurred in five of the eight behavioural categories (Table 7.1). Alert and pup interactions were the most robustly repeatable, with three out of the four analyses yielding significant repeatability estimates. Conversely, the locomotion, presenting & nursing and aggression behavioural categories were not repeatable in any of the four analyses. Where repeatability did occur across the 32 analyses, the estimates ranged from 0.49 to 0.8. The repeatability estimates of ICC3 were similar to those of ICC2 (Table A7.22), which suggests that there was little systematic change in females' behaviour across breeding seasons. As an indication of behavioural plasticity between breeding seasons the 1:1 line and the line of best fit was included in all pairwise plots (Figures 7.3, 7.5, 7.6 and A7.4, A7.5, A7.7, A7.8). However, the line of best fit for some of the plots is clearly influenced by widespread and/or outlying data points. The plots for the three years (Figure 7.4, A7.3 and A7.6) are harder to visually interpret since individuals do not always maintain rank order across breeding seasons (Hayes & Jenkins, 1997; Bell et al., 2009; Chapter 4, Section 4.2). Nevertheless, these plots show a varying degree of consistency between the five individuals for each of the three behavioural categories.

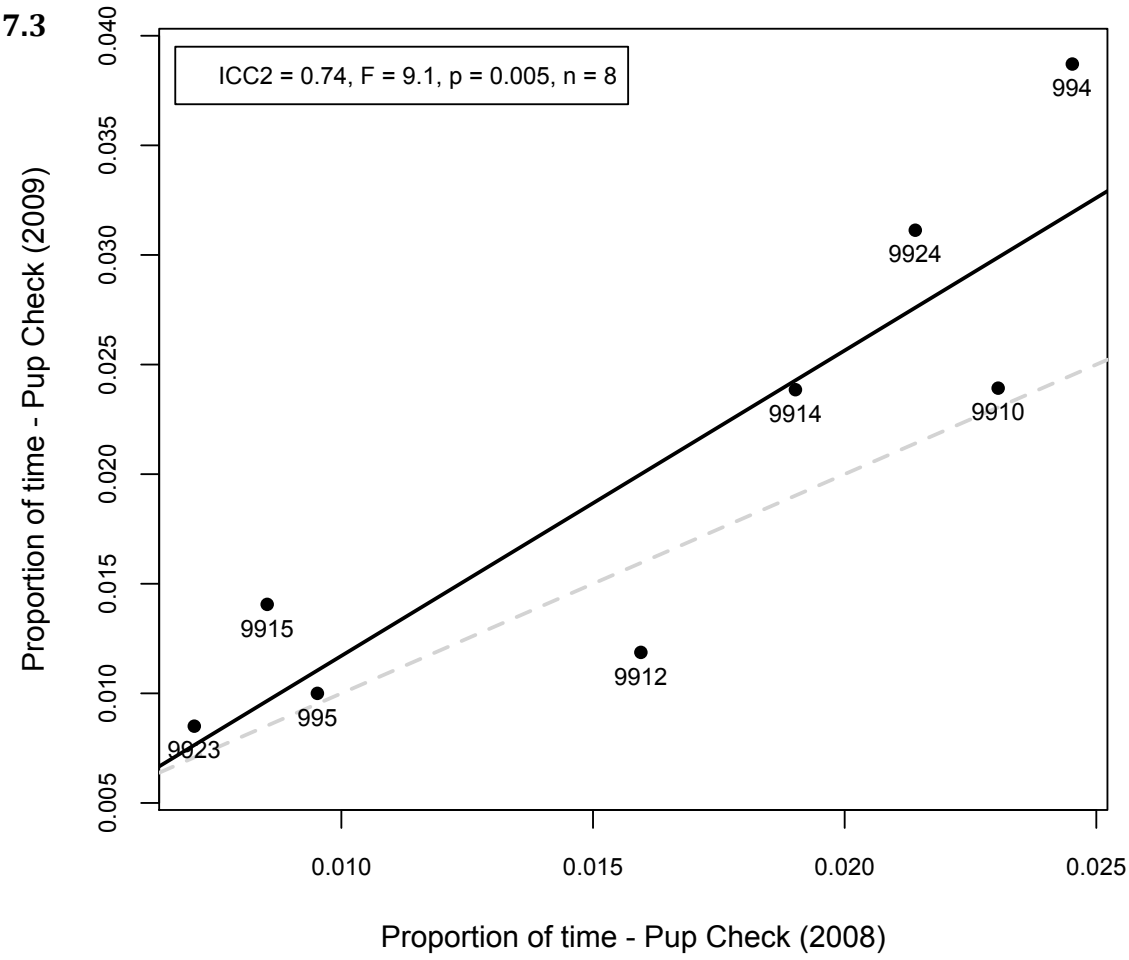
Table 7.1: ICC2 analyses for all 3 years (n = 5), 2008 & 2009 (n = 8), 2009 & 2010 (n = 12), 2008 & 2010 (n = 9). All significant results are in bold. Where ICC values are negative the best estimate for repeatability is zero (Hayes & Jenkins, 1997; Bell et al., 2009). See Table A7.22 for ICC3 results. The lower and upper columns show the 95% confidence limits.

Behaviour	Years	ICC	F	*p*	lower	upper
Resting	**2008 – 2010**	**0.67**	**7.6**	**0.008**	**0.17**	**0.95**
	2008 & 2009	0.29	2.1	0.18	-0.26	0.78
	2009 & 2010	**0.53**	**3.1**	**0.038**	**-0.069**	**0.84**
	2008 & 2010	0.53	3.3	0.054	-0.1	0.87
Comfort Movement	2008 – 2010	-0.14	0.65	0.65	-0.45	0.63
	2008 & 2009	**0.49**	**3.9**	**0.047**	**-0.12**	**0.86**
	2009 & 2010	-0.14	0.69	0.73	-0.52	0.38
	2008 & 2010	-0.17	0.6	0.76	-0.52	0.42
Pup Check	2008 – 2010	-0.26	0.29	0.87	-0.41	0.4
	2008 & 2009	**0.74**	**9.1**	**0.005**	**0.17**	**0.94**
	2009 & 2010	-0.29	0.33	0.96	-0.51	0.275
	2008 & 2010	0.085	1.3	0.36	-0.27	0.59
Alert	**2008 – 2010**	**0.6**	**6.2**	**0.014**	**0.099**	**0.94**
	2008 & 2009	0.32	2.1	0.18	-0.3	0.8
	2009 & 2010	**0.59**	**4.2**	**0.013**	**0.102**	**0.86**
	2008 & 2010	**0.8**	**8.2**	**0.004**	**0.3**	**0.95**
Locomotion	2008 – 2010	-0.14	0.58	0.68	-0.37	0.57
	2008 & 2009	0.31	1.9	0.21	-0.44	0.81
	2009 & 2010	0.21	1.5	0.24	-0.36	0.68
	2008 & 2010	-0.21	0.62	0.74	-0.69	0.46
Presenting & Nursing	2008 – 2010	0.41	3.8	0.051	-0.045	0.89
	2008 & 2009	0.015	1	0.49	-0.81	0.7
	2009 & 2010	0.26	1.8	0.17	-0.24	0.69
	2008 & 2010	0.33	2.1	0.16	-0.3	0.79
Pup Interaction	**2008 – 2010**	**0.56**	**4.4**	**0.037**	**-0.027**	**0.93**
	2008 & 2009	**0.52**	**4.7**	**0.029**	**-0.101**	**0.88**
	2009 & 2010	**0.5**	**2.9**	**0.046**	**-0.086**	**0.83**
	2008 & 2010	0.41	2.4	0.12	-0.28	0.83
Aggression	2008 – 2010	0.153	1.8	0.22	-0.15	0.77
	2008 & 2009	0.54	3.5	0.059	-0.12	0.88
	2009 & 2010	0.101	1.2	0.37	-0.44	0.61
	2008 & 2010	0.08	1.22	0.39	-0.38	0.63

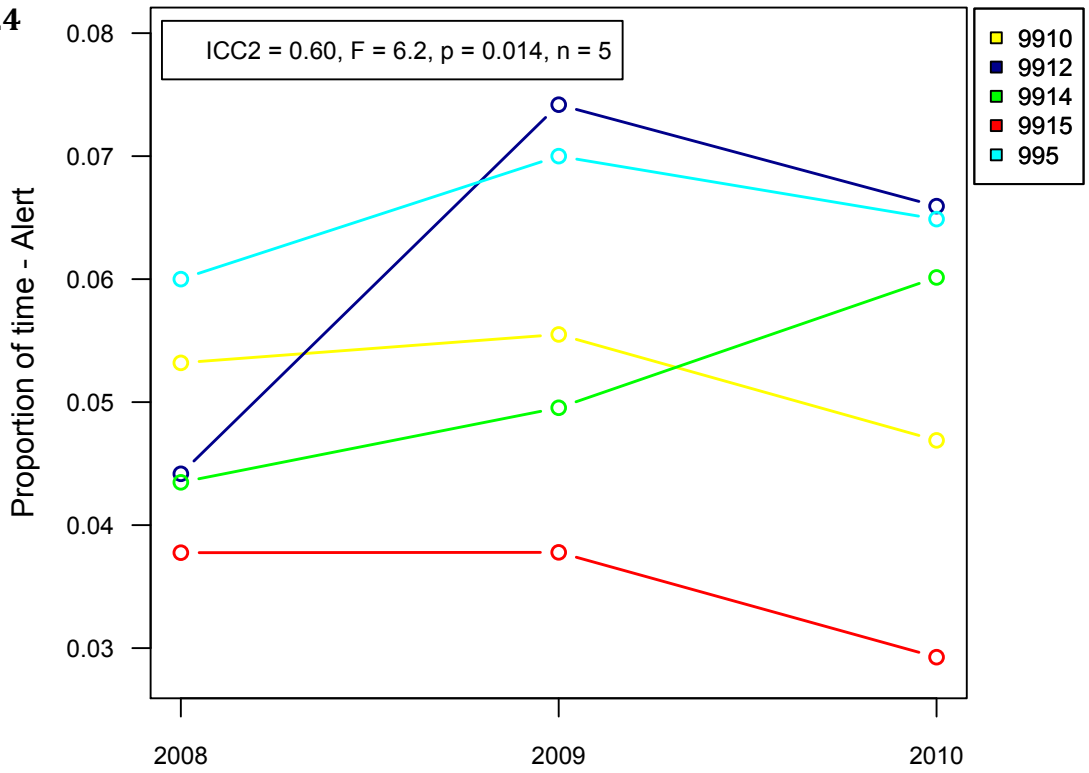
The following 2 pages show:

Figures 7.3 - 7.6: The plots of the significant repeatability estimates for the: **7.3**) pup check (2008 & 2009), **7.4, 7.5, 7.6**) and alert (2008 - 2010; 2009 & 2010; 2008 & 2010, respectively) behavioural categories. ICC2 results are shown in the legend within each of the plots. For the figures presenting three years of data the individuals' ID numbers are shown in the legend out-with the plot and are colour coded to the plotted lines. For the figures presenting two years of data the individuals' ID numbers are given for each data point. The line of best fit (black solid line) and the 1:1 line (grey dashed line) are presented in the pairwise plots.

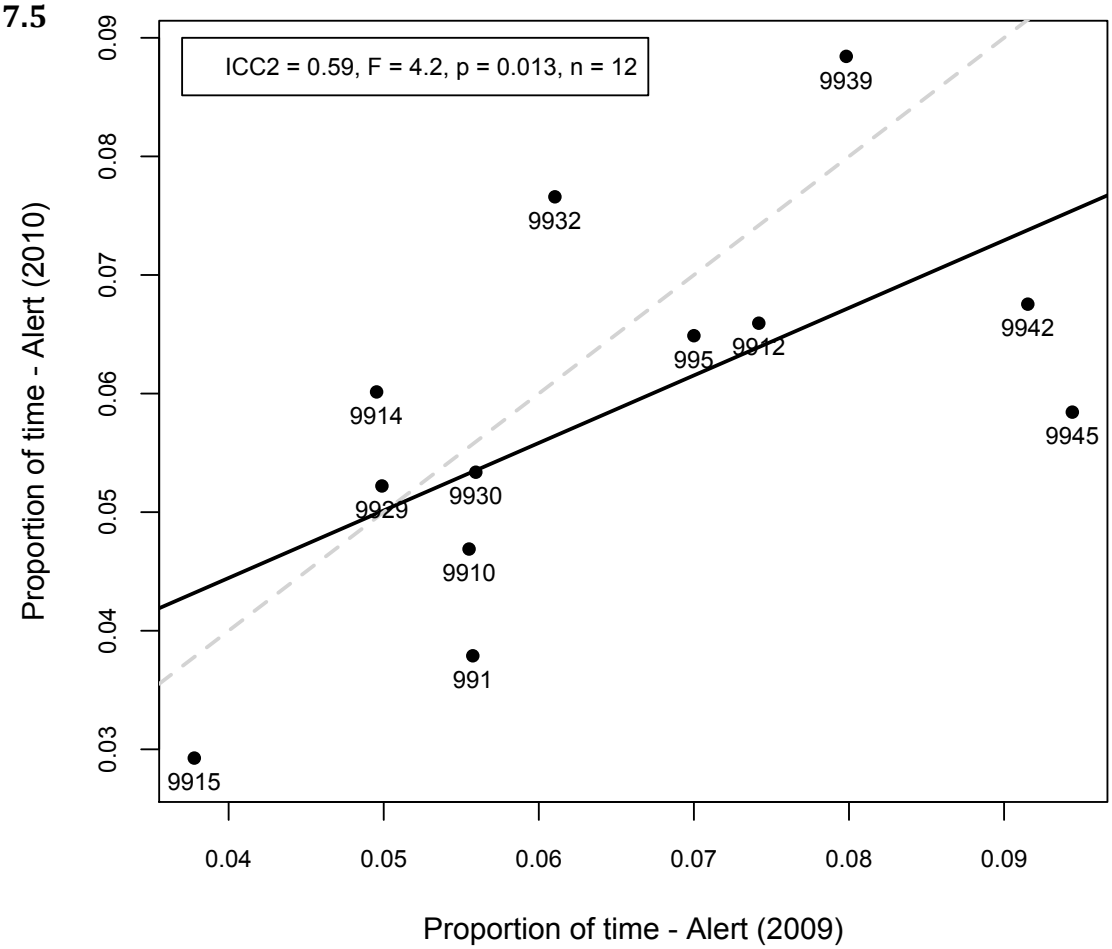
7.3


ICC2 = 0.74, F = 9.1, p = 0.005, n = 8
994
9924
9914
9910
9915
9912
995
9923
Proportion of time - Pup Check (2009)
Proportion of time - Pup Check (2008)
0.005
0.010
0.015
0.020
0.025
0.030
0.035
0.040

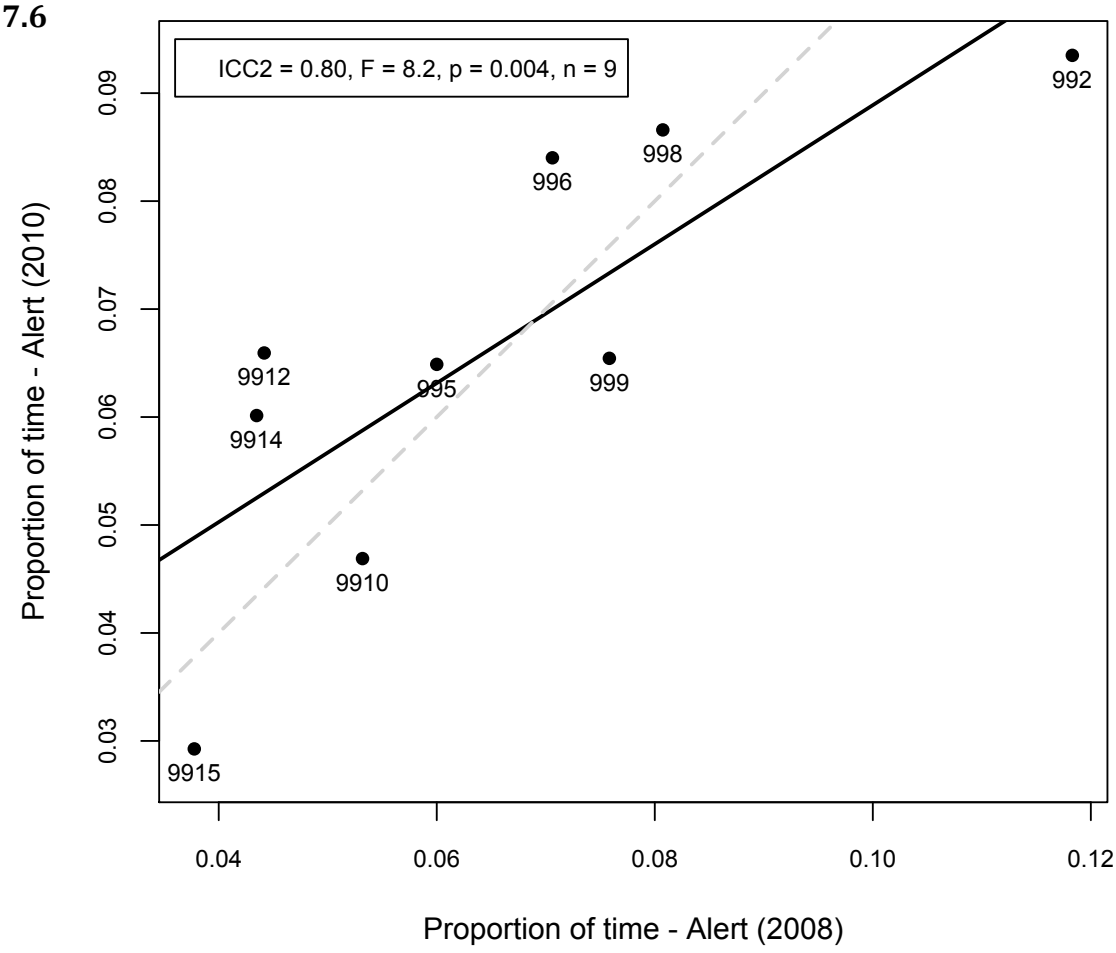
7.4


ICC2 = 0.60, F = 6.2, p = 0.014, n = 5
9910
9912
9914
9915
995
Proportion of time - Alert
0.03
0.04
0.05
0.06
0.07
0.08
2008
2009
2010

7.5


ICC2 = 0.59, F = 4.2, p = 0.013, n = 12
9939
9932
9942
995
9912
9914
9945
9929
9930
9910
991
9915
Proportion of time - Alert (2010)
Proportion of time - Alert (2009)
0.03
0.04
0.05
0.06
0.07
0.08
0.09

7.6


ICC2 = 0.80, F = 8.2, p = 0.004, n = 9
992
998
996
9912
995
999
9914
9910
9915
Proportion of time - Alert (2010)
Proportion of time - Alert (2008)
0.03
0.04
0.05
0.06
0.07
0.08
0.09
0.10
0.12

7.4.2. Step 2: The importance of individuals' ID as a fixed effect

The number of models retained at each of the 5 stages of the model selection process is shown in table A7.23. Collinearity occurred in 15 out of a possible 18 confidence sets. The number of models retained within the confidence sets across both behavioural categories ranged between 1 and 5 (median = 2), from a possible 127 (Tables 7.2 and 7.3). In the following sections the term 'fitted values' shall refer to the values extracted from the simplest model and the term 'predicted' values shall refer to those values predicted by the model whilst other influential covariates were standardised to their mean. For the plots presented henceforth, the 95% confidence intervals for the observed values are represented by error bars, whilst the 95% confidence intervals for the fitted values are represented by either error bars or dashed black lines. The subsequent sections shall present the results from the GLMs for the pup check and the alert behavioural categories, separately.

7.4.2.1. Pup check

There were 21 models retained across the nine confidence sets for the pup check behavioural category (Table 7.2). Individuals' ID was retained in relatively few of these models (3/21). Of the continuous covariates retained across the confidence sets, the greatest support was for the activity of the pup, which was retained in two thirds of the models (14/21). There was also limited support for pup age (4/21), density (3/21), distance to the nearest female neighbour (3/21) and air temperature (4/21). However, across datasets, air temperature had both a positive and a negative relationship with the pup checking behaviour. With the exception of the activity of the pup, which was retained in the three confidence sets for the 2009 and 2010 breeding seasons, no other covariate was retained in the three confidence sets for a given year. The pup activity was typically influential; however, the estimates for this covariate in the 2008 datasets was close to or less than half the standard error of the estimate. Of the other covariates retained in the 21 models, all had an estimate that was greater than twice the standard error, with one exception (2008 & 2009; 2008: air temperature, estimate = 0.05, SE = 0.049).

Table 7.2: The summary for each of the models that were retained within the confidence set for individuals that were re-sighted in all three years (2008 - 2010; n = 5), 2008 & 2009 (n = 8), 2009 & 2010 (n = 11) and 2008 & 2010 (n = 9) for the **pup check behavioural category** (the number of models that were retained at each of the 5 stages of the model selection process is shown in Table A7.23). The models are arranged using the △ value; the AICc value is not presented. With the exception of ID, if the covariate was retained within the model then the estimated effect (Est.) and the standard error of the estimate (SE) are included in the table. ID is a categorical covariate; it was only of interest to know whether it was retained (✓) or not (X). Where ID was not retained within the confidence set the 'best' model containing this covariate is presented in bold italics in the last row of each of the confidence sets, irrespective of its △ value. See the footnote for definitions of the covariates and of abbreviations. The covariate POOL was not retained in any of the models within the nine confidence sets, and was therefore omitted from the table. Table 7.2 is continued overleaf.

						Covariates												
		Intercept		ODC		ACT		AGE		DEN		NFN		TEMP		ID		
Analyses	Year	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE		d.f.	△
2008 –	2008	-3.204	0.338	0.022	0.144	-	-	-	-	-	-	-0.181	0.060	-	-	X	3	0
2010		***-3.154***	***0.682***	***0.022***	***0.015***	**-**	**-**	**-**	**-**	**-**	**-**	***-0.181***	***0.084***	**-**	**-**	✓	***7***	***6.296***
	2009	-4.551	0.220	0.021	0.012	1.246	0.497	-	-	-	-	-	-	-	-	X	3	0
		-4.917	***0.394***	***0.019***	***0.012***	***1.168***	***0.519***	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	✓	***7***	***1.521***
	2010	-2.980	0.257	0.003	0.009	1.010	0.325	-0.071	0.020	-	-	-	-	-	-	✓	8	0
		-3.297	0.209	0.007	0.009	0.986	0.323	-0.07	0.021	-	-	-	-	-	-	X	4	0.380
2008 &	2008	-3.844	0.300	0.017	0.010	0.961	0.465	-	-	-	-	-0.130	0.052	-	-	X	4	0
2009		-3.619	0.275	0.019	0.011	-	-	-	-	-	-	-0.123	0.052	-	-	X	3	1.88
		-4.933	0.290	0.019	0.010	0.962	0.469	-	-	0.121	0.055	-	-	-	-	X	4	2.293

		-4.641	0.244	0.021	0.011	-	-	-	-	0.111	0.055	-	-	-	-	X	3	4.128
		-4.482	0.190	0.019	0.011	0.880	0.474	-	-	-	-	-	-	-	-	X	3	5.022
		-3.731	***0.506***	***0.013***	***0.010***	***1.073***	***0.471***	***-***	***-***	***-***	***-***	***-0.131***	***0.071***	***-***	***-***	✓	***11***	***4.663***
	2009	-3.242	0.325	0.019	0.011	0.930	0.428	-	-	-	-	-	-	-	-	✓	10	0
		-3.002	0.302	0.022	0.011	-	-	-	-	-	-	-	-	-	-	✓	9	1.872
		-3.265	0.485	0.022	0.010	0.979	0.419	-	-	-	-	-	-	-0.108	0.049	X	4	2.162
		-4.298	0.178	0.024	0.011	0.926	0.421	-	-	-	-	-	-	-	-	X	3	5.033
		-3.042	0.477	0.024	0.011	-	-	-	-	-	-	-	-	-0.102	0.049	X	3	5.182
2009 &	2009	-4.537	0.155	0.011	0.007	1.286	0.371	-	-	-	-	-	-	-	-	X	3	0
2010		***-5.066***	***0.379***	***0.009***	***0.007***	***1.33***	***0.387***	***-***	***-***	***-***	***-***	***-***	***-***	***-***	***-***	✓	***13***	***7.278***
	2010	-4.177	0.139	0.013	0.007	1.287	0.248	-	-	0.009	0.033	-	-	-	-	X	4	0
		-3.963	0.110	0.015	0.007	1.302	0.250	-	-	-	-	-	-	-	-	X	3	4.712
		-4.072	***0.224***	***0.010***	***0.007***	***1.243***	***0.256***	***-***	***-***	***0.104***	***0.041***	***-***	***-***	***-***	***-***	✓	***14***	***9.464***
2008 &	2008	-3.429	0.219	0.025	0.011	-	-	-0.057	0.022	-	-	-	-	-	-	X	3	0
2010		-4.484	0.529	0.027	0.011	-	-	-	-	-	-	-	-	0.05	0.049	X	3	5.719
		-2.633	***0.352***	***0.018***	***0.010***	***-***	***-***	***-0.07***	***0.024***	***-***	***-***	***-***	***-***	***-***	***-***	✓	***11***	***0.740***
	2010	-3.439	0.161	0.014	0.007	1.158	0.231	-0.046	0.013	-	-	-	-	-	-	X	4	0
		-4.975	0.424	0.014	0.007	1.233	0.232	-	-	-	-	-	-	0.101	0.038	X	4	5.196
		-3.508	***0.257***	***0.011***	***0.007***	***1.148***	***0.236***	***-0.053***	***0.013***	***-***	***-***	***-***	***-***	***-***	***-***	✓	***12***	***4.061***

ACT: proportion of time the pup spent active; **AGE:** age of pup (days postpartum); **DEN:** the number of females within a 10 m buffer zone of the target female; **NFN**: the distance between a mother and her nearest female neighbour (m); **POOL**: the distance between a mother and her nearest pool (m); **TEMP**: air temperature (^{o}C); **ID**: Individuals' identification code. ACT and TEMP were recorded at hourly intervals; AGE, DEN, NFN and POOL were recorded at daily intervals; **ODC**: overdispersion coefficient; **d.f**: degrees of freedom.

Therefore, the simplest model varied between datasets, which made general inference across breeding seasons and/or groups of re-sighted individuals difficult.

Step 1 found that the pup check behaviour was repeatable for the individuals that were re-sighted in 2008 & 2009 (Table 7.1); therefore, the simplest models for these datasets shall be plotted. However, in 2008, individuals' ID was not retained in any model within the confidence set (Table 7.2); therefore, the 'best' model out-with the confidence set, which retained individuals' ID was used. This model also retained pup activity and the distance to the nearest female neighbour; the former had a positive relationship and was influential, the latter had a negative relationship and was not influential. In 2009, the simplest model contained only the individuals' ID. The 2010 dataset for the individuals re-sighted in 2008 - 2010 shall also be plotted, because this was the only other confidence set in which individuals' ID was retained. The simplest model for 2010 retained pup activity and pup age; the former had a positive relationship, the latter had a negative relationship, both were influential.

For the majority of the pup check models, the estimate for the overdispersion coefficient was always less than twice the standard error. Therefore, the additional binomial error provided by the beta-binomial distribution was not required (see Chapter 5, Appendix, Section A). Nevertheless, the goodness-of-fit plots showed that the observed frequency of pup checking behaviour fitted the beta-binomial distribution well (Figure A7.9). However, for individuals with greater variance in their behaviour and/or with a smaller number of scan samples, the fitted and the predicted values tended to considerably under or over estimate the occurrence of the pup checking behaviour (Figure 7.7). For the 2008 and 2010 datasets, Where the activity of the pup was standardised to its mean, the accuracy of the predictions in relation to the mean observed and mean fitted values deviated more for some individuals than others (only individuals' ID, was retained in the simplest model for the 2009 dataset, therefore there are no additional covariates to standardise to their mean).

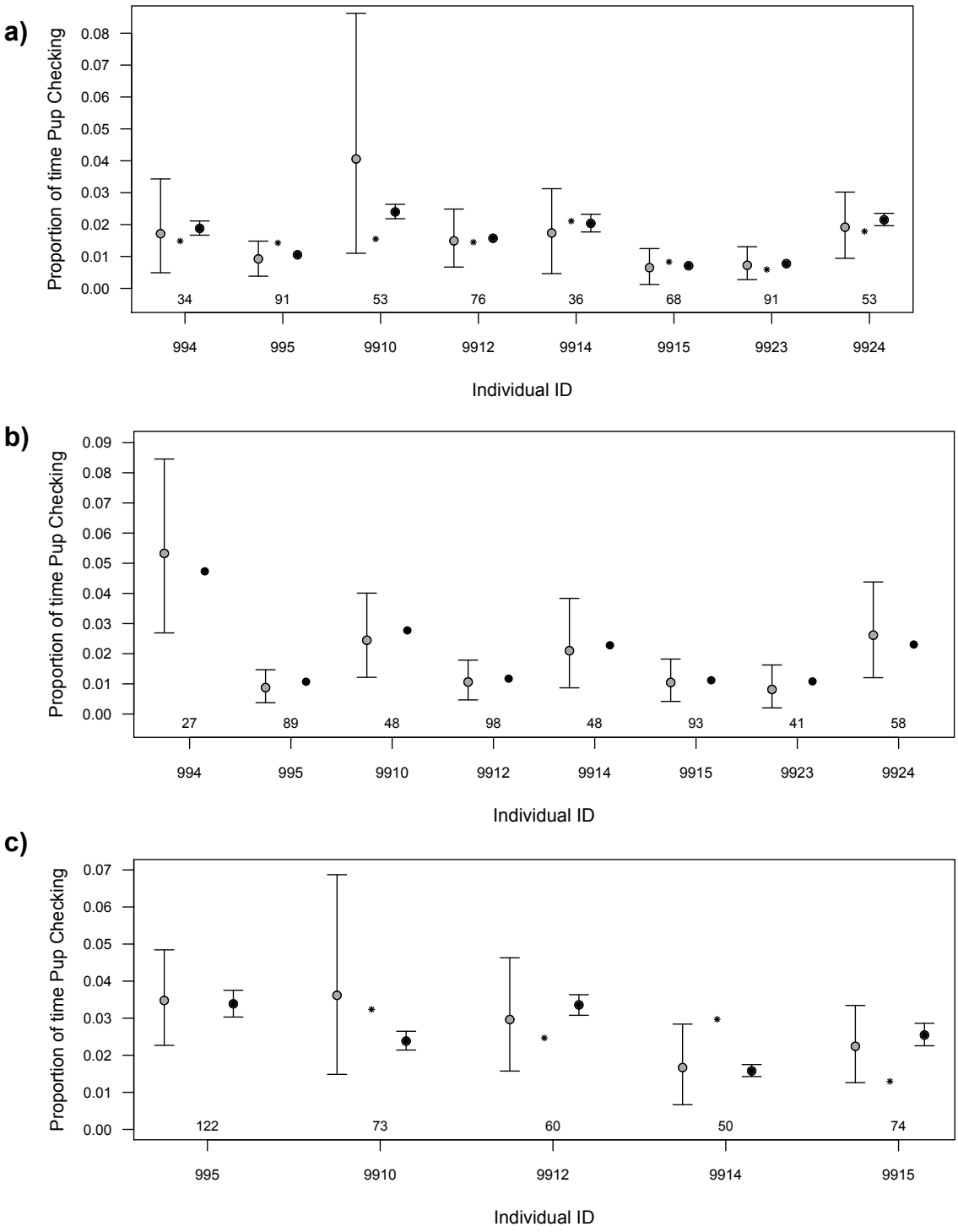


Figure 7.7: The mean observed (grey) and the mean fitted (black) proportion of time that each of the re-sighted individuals spent pup checking in the **a)** 2008 **b)** 2009 (2008 & 2009 re-sighted individuals) and **c)** 2010 (2008 - 2010 re-sighted individuals) breeding seasons; * indicates the predicted value for each individual whilst the other covariates retained within the model were standardised to their mean. For **b)** only individuals' ID was retained; therefore, there is only one fitted value per individual and no predicted value. The total number of hours that each individual was observed is noted on the inside of the x-axis. The covariates retained in each of these models are noted in Section 7.4.2.1.

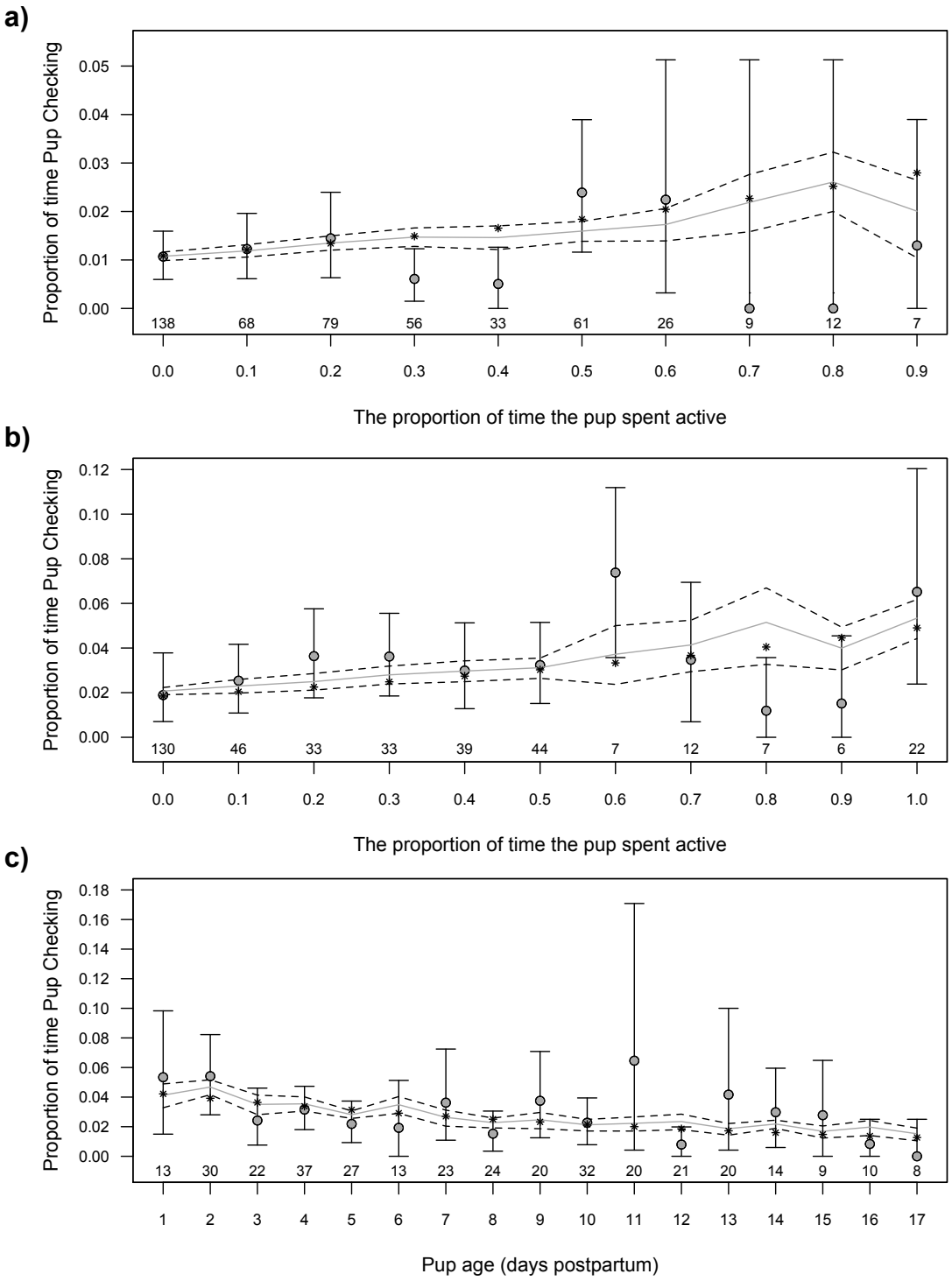


Figure 7.8: The mean observed (grey dots) and the mean fitted (grey line) proportion of time females spent pup checking in the **a)** 2008 (2008 & 2009 re-sighted individuals) and **b)** 2010 (2008 - 2010 re-sighted individuals) breeding seasons across the observed range of pup activity; and **c)** 2010 breeding season across the observed range of pup age; * indicates the predicted value for each bin of data whilst the other covariates were standardised to their mean. The value on the inside of the x-axis shows the number of data points (hourly scan samples) within the respective bin. For **a)** there were too few observed data where the proportion of pup activity = 1.0; therefore, the range of pup activity modelled was 0 - 0.9. The covariates retained in each of these models are noted in Section 7.4.2.1.

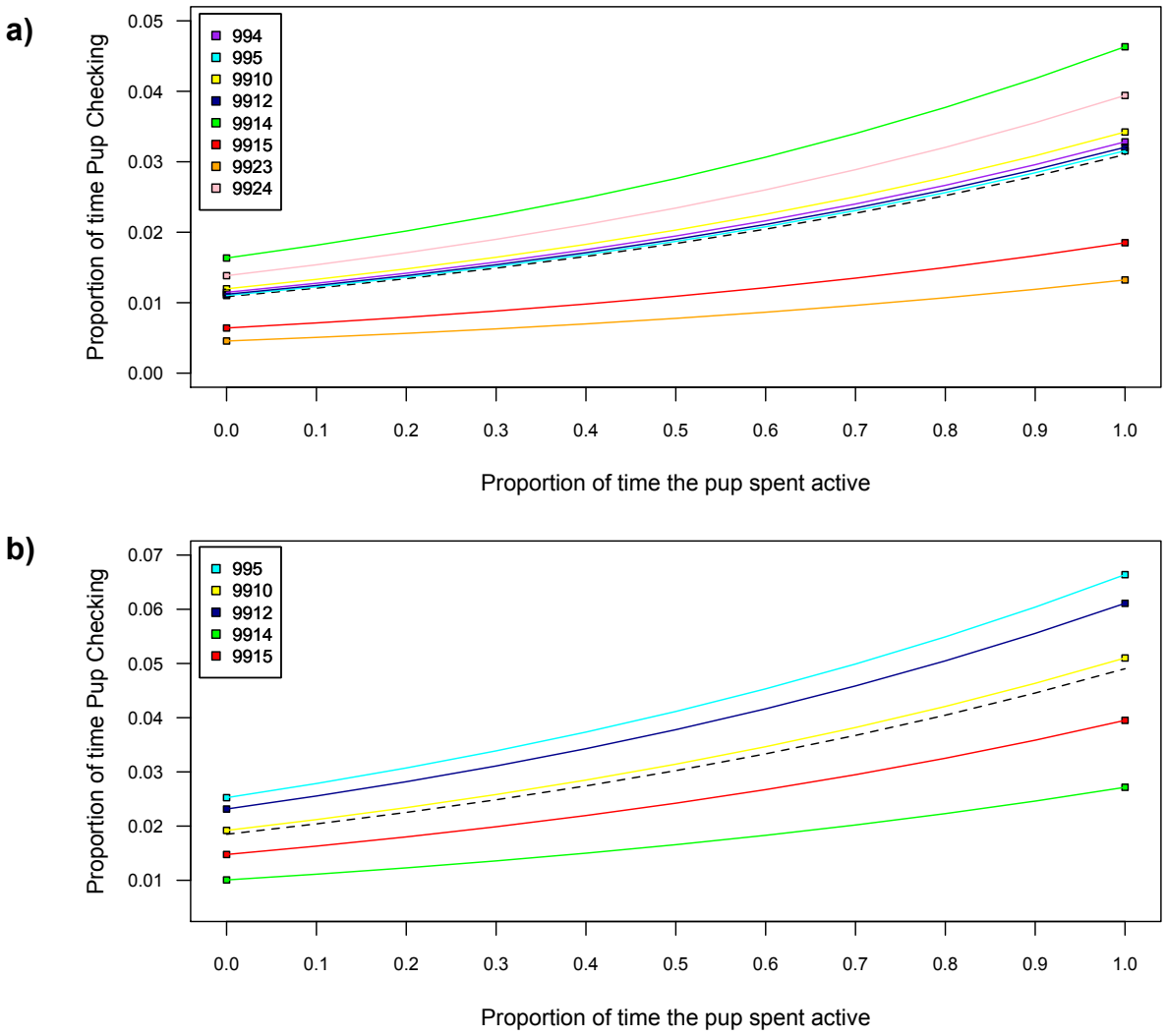


Figure 7.9: The predicted values for the proportion of time each individual spent pup checking in the **a)** 2008 (2008 & 2009 re-sighted individuals) and **b)** 2010 (2008 - 2010 re-sighted individuals) breeding seasons across the observed range of pup activity. The mean of the group is shown as the black dashed line. Each individual has a unique colour code, which is shown in the legend inside the figure, and is maintained throughout the plots presented in this chapter.

For the 2008 and 2010 datasets, the models showed that as the pup becomes more active, the mother spends more time pup checking (Table 7.2; Figures 7.8a, b). For the most part, the models predicted these data relatively well; however, the pattern was less pronounced at greater proportions of pup activity, which is shown in the increase in the 95% confidence intervals for both the observed and fitted values. Where the average proportion of time spent pup

checking for the group of re-sighted individuals was used, the predicted values were similar to the mean fitted values. This was particularly true for the mean fitted values at higher proportions of pup activity (Figures 7.8a, b). For the 2010 dataset, the model showed that the older the pup was, the less time the mother spent pup checking (Figure 7.8c). The model fitted the general pattern in the observed data for the earlier days postpartum, where a clear downward trend was apparent. However, throughout the 17 days postpartum, the mean observed values were often out-with the 95% confidence intervals for the fitted vales. The unconvincing fit is also mirrored in the predicted values, which were typically similar to the mean fitted values (Figure 7.8c).

The plots for the predicted proportion of time spent pup checking for each individual across the observed range of pup activity for the 2008 and 2010 datasets reiterates that substantial levels of individual variation in this behaviour for these re-sighted individuals' datasets did occur, and that the activity of the pup was considerably influential (Figure 7.9). Furthermore, despite the relatively small number of females, these individuals did span the entire range of the between-individual variation. For the 2010 breeding season, the model generally failed to fit (or predict) the observed proportion of time spent pup checking across the observed range of pup age (Figure 7.8c). Consequently, the predicted proportion of time spent pup checking for each individual across the observed range of pup age was not presented.

7.4.2.2. Alert

There were 16 models retained across the nine confidence sets for the alert behavioural category (Table 7.3). Individuals' ID was retained in approximately two thirds of these models (11/16). Of the continuous covariates retained across the confidence sets, the greatest support was for the activity of the pup, which was retained in all of the models (16/16). There was also limited support for the pup age (5/16), density (3/16), distance to the nearest female neighbour (3/16) and air temperature (2/16). With the exception of the activity of the pup (which always had a positive, influential relationship with the alert behaviour), the only other covariat

Table 7.3: The summary for each of the models that were retained within the confidence set for individuals that were re-sighted in all three years (2008 - 2010; n = 5), 2008 & 2009 (n = 8), 2009 & 2010 (n = 11) and 2008 & 2010 (n = 9) for the **alert behavioural category** (the number of models that were retained at each of the 5 stages of the model selection process is shown in Table A7.23). The covariate POOL was not retained in any of the models within the nine confidence sets, and was therefore omitted from the table. See Table 7.2 for the complete table legend, and see the footnote for Table 7.2 for definitions of the covariates and of abbreviations. Table 7.3 is continued overleaf.

						Covariate												
		Intercept		ODC		ACT		AGE		DEN		NFN		TEMP		ID		
Analyses	Year	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE		d.f.	Δ
2008 -	2008	-2.953	0.281	0.015	0.010	1.177	0.317	0.028	0.017	-	-	-0.100	0.030	-	-	X	5	0
2010		-2.656	0.210	0.015	0.010	1.139	0.317	-	-	-		-0.101	0.030	-	-	X	4	0.696
		-1.811	0.488	0.014	0.010	1.030	0.319	-	-	-	-	-	-	-0.129	0.042	✓	8	5.142
	2009	-1.643	0.445	0.042	0.013	1.513	0.292	-	-	-	-	-	-	-	-	✓	8	0
	2010	-3.074	0.229	0.028	0.011	1.756	0.254	-0.03	0.016	-	-	-	-	-	-	✓	8	0
		-3.384	0.174	0.028	0.011	1.768	0.253	-	-	-	-	-	-	-	-	✓	7	1.564
		-3.626	0.155	0.032	0.011	1.670	0.247	-	-	0.084	0.031	-	-	-	-	X	4	3.825
2008 &	2008	-2.904	0.167	0.020	0.009	1.373	0.247	-	-	-	-	-0.076	0.026	-	-	X	4	0
2009		-3.694	0.181	0.021	0.009	1.366	0.250	0.039	0.014	-	-	-	-	-	-	X	4	1.426
		-3.447	***0.281***	***0.018***	***0.008***	***1.393***	***0.247***	***0.045***	***0.015***	***-***	***-***	***-***	***-***	***-***	***-***	✓	***11***	***7.128***
	2009	-1.572	0.341	0.035	0.010	1.372	0.251	-	-	-	-	-	-	-0.125	0.036	✓	11	0
2009 &	2009	-3.069	0.184	0.044	0.009	1.312	0.221	-	-	0.038	0.023	-	-	-	-	✓	14	0
2010		-2.945	0.172	0.044	0.009	1.270	0.219	-	-	-	-	-	-	-	-	✓	13	0.564

	2010	-3.360	0.160	0.032	0.008	1.713	0.191	-	-	-	-	-	-	-	-	✓	13	0
2008 &	2008	-2.888	0.229	0.018	0.008	1.494	0.214	0.051	0.013	-	-	-	-	-	-	✓	12	0
2010	2010	-2.606	0.131	0.035	0.008	1.373	0.175	-	-	0.05	0.029	-	-	-	-	✓	12	0
		-2.552	0.128	0.035	0.008	1.367	0.176	-	-	-	-	-	-	-	-	✓	11	1.291

retained in the three confidence sets for the same breeding season was pup age in 2008. However, across breeding seasons, pup age had both a positive and a negative relationship. Both the distance to the nearest female neighbour and the air temperature had a negative relationship, and were always influential. The influence of the pup age and the density was variable (2/5 and 1/3 were considered influential, respectively). Consequently, the simplest model varied between datasets, which made general inference across breeding seasons and/or groups of re-sighted individuals difficult.

Step 1 found that the alert behaviour was repeatable for three of the four re-sighted individuals' datasets (Table 7.1). Of these, the 2008 & 2010 re-sighted individuals had the highest repeatability estimate; therefore, the simplest models for these datasets shall be plotted. In 2008, the simplest model was individuals' ID, pup activity and pup age (both of which had a positive, influential relationship; Table 7.3). In 2010, the simplest model was individuals' ID and pup activity. To give an example of a dataset from the 2009 breeding season, the 2009 & 2010 re-sighted individuals were used. This dataset was selected because it maximised the sample size of individuals. The simplest model for 2009 also included individuals' ID and pup activity.

For the majority of the alert models, the estimate for the overdispersion coefficient was always more than twice the standard error. Therefore, the additional binomial error provided by the beta-binomial distribution did improve the model fit (Chapter 5, Appendix, Section A). This is supported by the goodness-of-fit plots, which show that the observed frequency of the alert behaviour fitted the beta-binomial distribution well (Figure A7.10). The between- and within-individual variation in the alert behaviour was evident from the plots of the observed data (Figure 7.10). The model fitted these data well, although the within-individual variation was typically less for the fitted values. Where the activity of the pup was standardised to its mean, the predicted values were typically similar to the mean observed and mean fitted values. However, for some individuals, particularly those with greater within-individual variation, the predicted values tended to deviate further from the mean observed and mean fitted values (Figure 7.10).

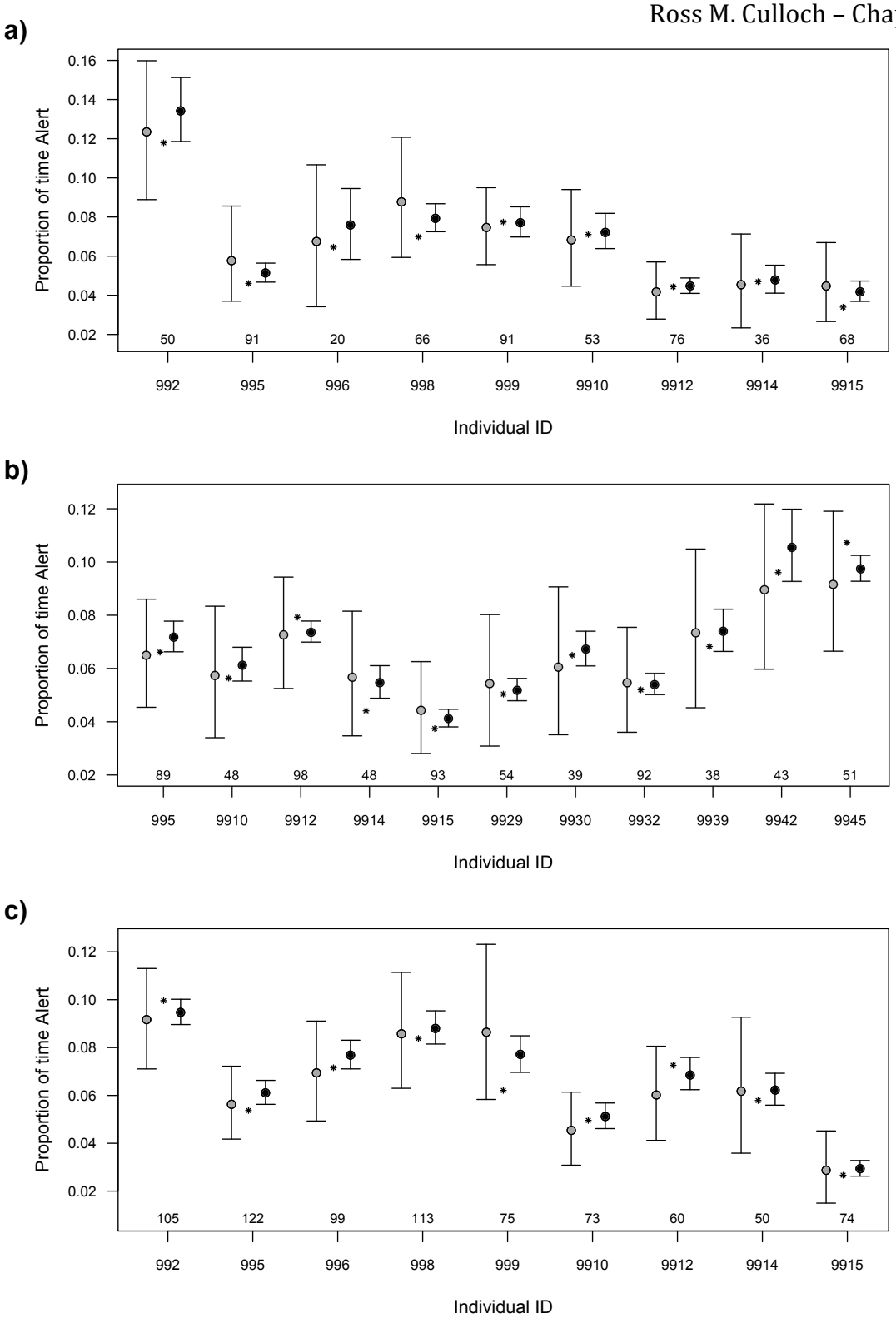


Figure 7.10: The mean observed (grey) and the mean fitted (black) proportion of time that each of the re-sighted individuals spent alert in the **a)** 2008 (2008 & 2010 re-sighted individuals) **b)** 2009 (2009 & 2010 re-sighted individuals) and **c)** 2010 (2008 & 2010 re-sighted individuals) breeding seasons; * indicates the predicted value for each individual whilst the other covariates were standardised to their mean. The total number of hours that each individual was observed is noted on the inside of the x-axis. The covariates retained in each of these models are noted in Section 7.4.2.2.

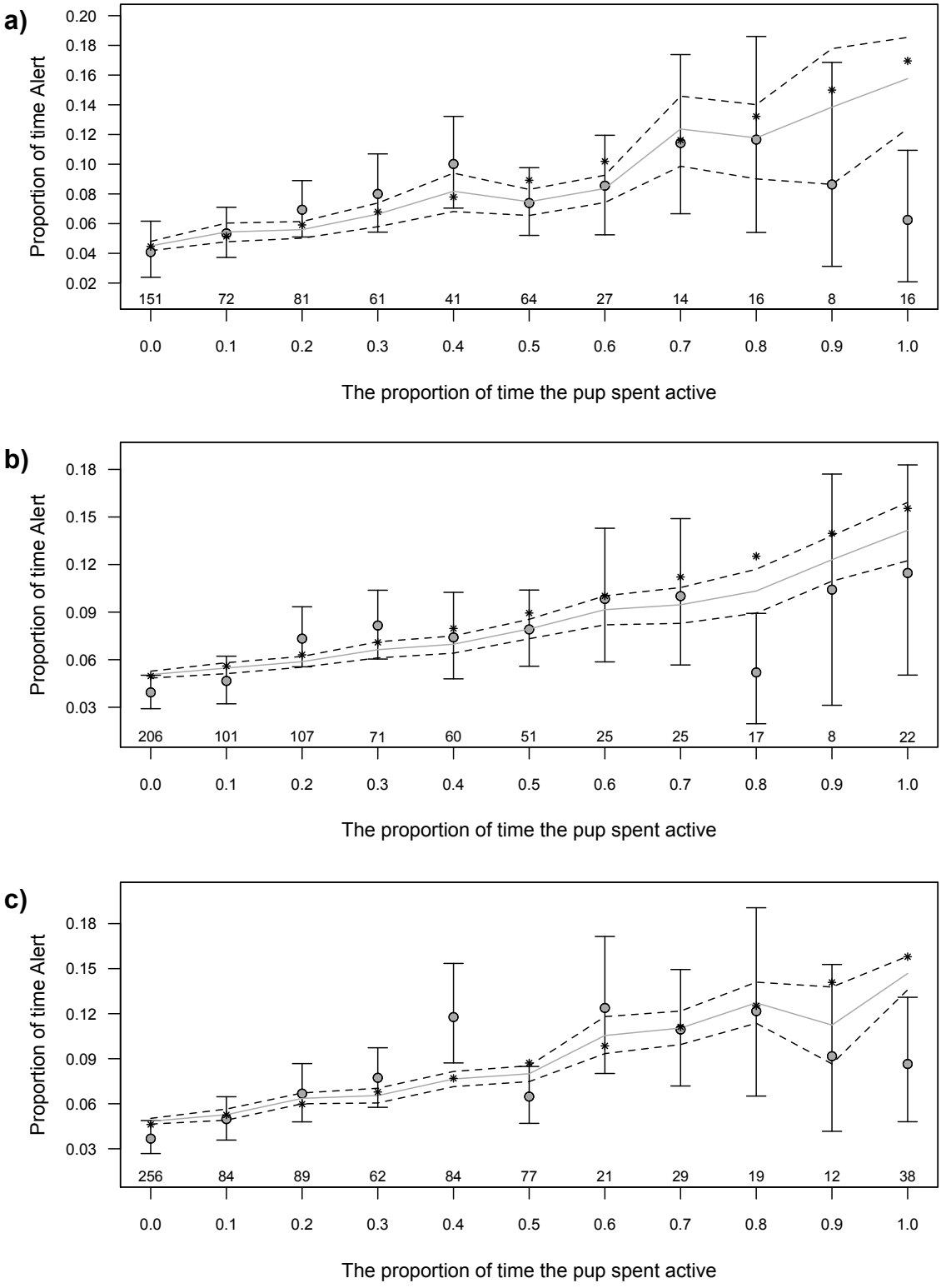


Figure 7.11: The mean observed (grey dots) and the mean fitted (grey line) proportion of time females spent alert in the **a)** 2008 (2008 & 2010 re-sighted individuals) **b)** 2009 (2009 & 2010 re-sighted individuals) and **c)** 2010 (2008 & 2010 re-sighted individuals) breeding seasons across the observed range of pup activity; * indicates the predicted value for each bin of data whilst the other covariates were standardised to their mean. The value on the inside of the x-axis shows the number of data points (hourly scan samples) within the respective bin. The covariates retained in each of these models are noted in Section 7.4.2.2.

The models showed that as the pup became more active, the mother spent more time alert (Table 7.3; Figure 7.11). For the most part, the models predicted these data well. However, at higher proportions of time spent active, there was an increase in the 95% confidence intervals for both the observed and fitted values. Furthermore, in 2008 and in 2010 the observed proportion of time spent alert appeared to decrease when pup activity was ≥ 0.8, which was not captured by the model. Where the average proportion of time spent alert for the group of re-sighted individuals was used, the predicted values were similar to the mean fitted and mean observed values. However, at higher proportions of time spent active by the pup, the predicted values tended to overestimate the proportion of time the mother spent alert (Figure 7.11). The model for the 2008 breeding season did not fit the pup age data well, and this was also reflected in the predicted values, which typically underestimated the proportion of time spent alert during the early and late stages of lactation (Figure 7.12).

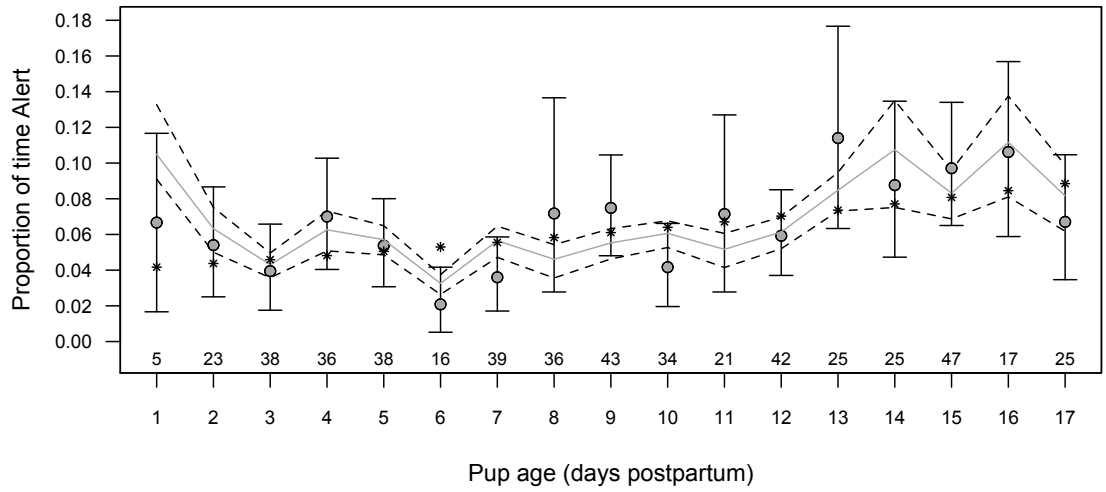


Figure 7.12: The mean observed (grey dots) and the mean fitted (grey line) proportion of time females spent alert in the 2008 (2008 & 2010 re-sighted individuals) breeding season across the observed range of pup age; * indicates the predicted value for each bin of data whilst the other covariates were standardised to their mean. The value on the inside of the x-axis shows the number of data points (hourly scan samples) within the respective bin. The covariates retained in each of these models are noted in Section 7.4.2.2.

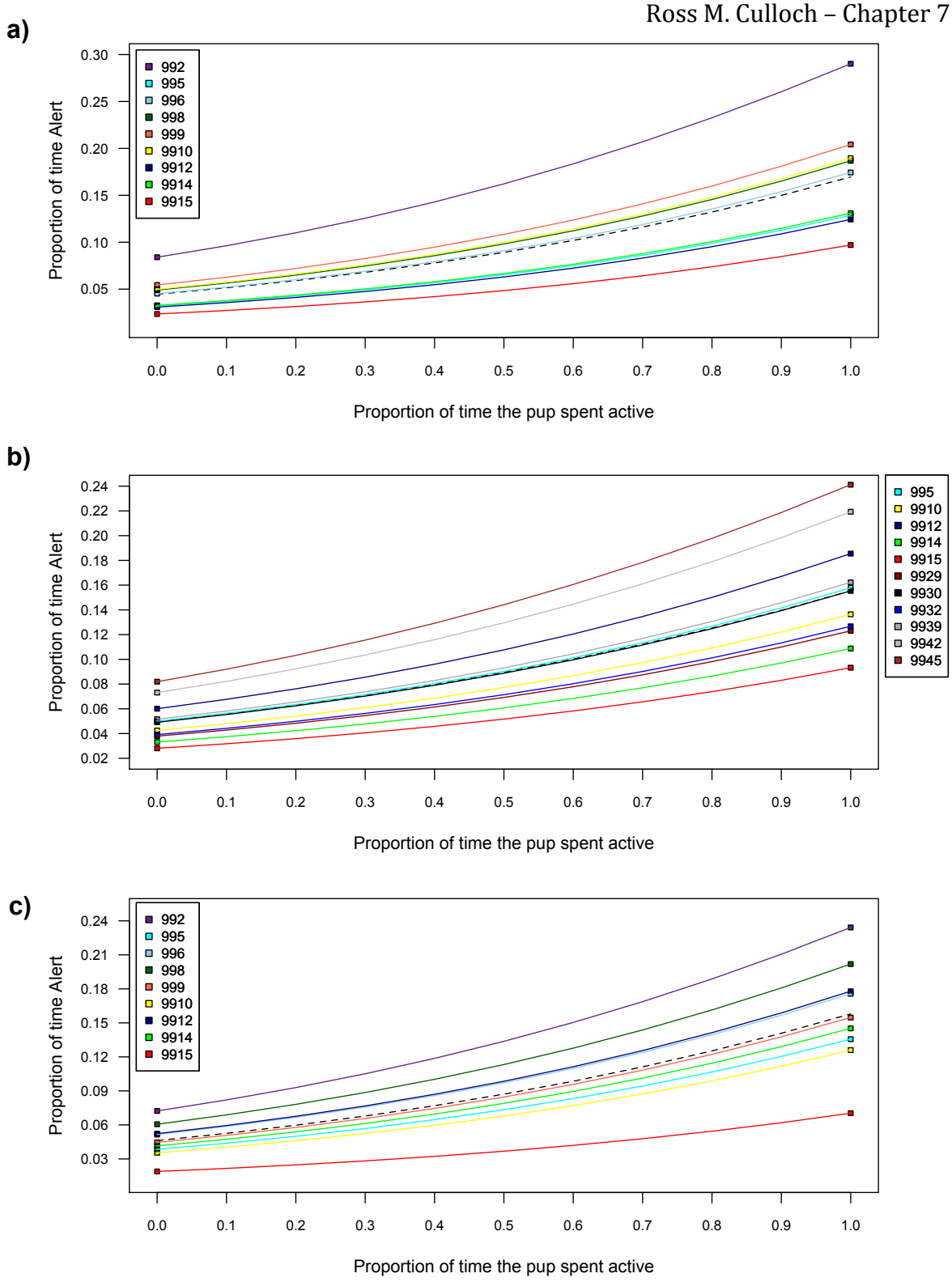


Figure 7.13: The predicted values for the proportion of time each individual spent alert in the **a)** 2008 (2008 & 2010 re-sighted individuals) **b)** 2009 (2009 & 2010 re-sighted individuals) and **c)** 2010 (2008 & 2010 re-sighted individuals) breeding seasons across the observed range of pup activity The mean of the group is shown as the black dashed line. Each individual has a unique colour code, which is shown in the legend, and is maintained throughout the plots presented in this chapter.

The plots for the predicted proportion of time spent alert for each individual across the observed range of pup activity, reiterates that substantial levels of individual variation in this behaviour for these re-sighted individuals' datasets did occur, and that the activity of the pup was considerably influential (Figure 7.13). In the 2009 plot, the individuals did span the entire range of the between-individual variation. Whereas for the 2008 and 2010 plots there was one individual (992 and 9915, respectively) that considerably increased the between-individual variation. For the 2008 breeding season, the model generally failed to fit (or predict) the observed proportion of time spent alert across the observed range of pup age (Figure 7.12). Consequently, the predicted proportion of time spent alert for each individual across the observed range of pup age was not presented.

7.4.3. Step 3: Quantifying the repeatability of behaviour after accounting for influential covariates

The number of models retained at each of the 5 stages of the model selection process is shown in Table A7.24. Collinearity occurred in 11 out of a possible 18 confidence sets. Considering all of the re-sighted individuals' datasets, the number of models retained within the confidence sets ranged between 1 and 4 (median = 1) from a possible 63 (Tables 7.4 and 7.6). The goodness-of-fit plots showed that the observed frequency of the pup check behaviour fitted the binomial distribution well (Figure A7.11). However, for the alert behaviour, these plots showed that the model tended to overestimate occurrences ≤ 1 and underestimate occurrences > 1 (Figure A7.12). The subsequent sections shall present the results from the GLMMs for the pup check and the alert behavioural categories, separately.

7.4.3.1. Pup check

There were 15 models retained across the nine confidence sets for the pup check behavioural category. Across all 15 models, the estimated variance of the individuals' ID ranged from 0 to 0.187 (Table 7.4). The activity of the pup was retained in the majority of the models across all of the confidence sets (11/15). There was also limited support for pup age (4/15), the distance to the nearest

Table 7.4: The summary for each of the models that were retained within the confidence set for individuals that were re-sighted in all three years (2008 - 2010; n = 5), 2008 & 2009 (n = 8), 2009 & 2010 (n = 11) and 2008 & 2010 (n = 9) for the **pup check behavioural category** (the number of models that were retained at each of the 5 stages of the model selection process is shown in Table A7.24). The models are arranged using the △ value; the AIC value is not presented. If the covariate was retained within the model then the estimated effect (Est.) and the standard error of the estimate (SE) are included in the table. ID was included as a random effect; the variance explained (Var.) and the standard deviation (SD) are included in the table. Models in bold are the simplest model (with the lowest AIC) within the respective confidence set. See the footnote of Table 7.2 for definitions of the covariates. The covariate POOL was not retained in any of the models within the nine confidence sets, and was therefore omitted from the table. The model number (No.) relates to the ICC analyses (Table A7.25). Table 7.4 is continued overleaf.

					Covariates												
			Intercept		**ID**		**ACT**		**AGE**		**DEN**		**NFN**		**TEMP**		
Analyses	**Year**	**No.**	**Est.**	**SE**	**Var.**	**SD**	**Est.**	**SE**	**Est.**	**SE**	**Est.**	**SE**	**-0200**	**0.057**	**Est.**	**SE**	△
2008 - 2010	2008	**1**	**-3.136**	**0.312**	**0**	**0**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**0**
	2009	**1**	**-4.568**	**0.240**	**0.070**	**0.264**	**1.352**	**0.468**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**0**
	2010	**1**	**-3.295**	**0.221**	**0.040**	**0.200**	**0.972**	**0.319**	**-0.076**	**0.020**	**-**	**-**	-	-	**-**	**-**	**0**
2008 & 2009	2008	1	-3.863	0.320	0.054	0.233	1.148	0.435	-	-	-	-	-0.138	0.054	-	-	0
		2	-4.897	0.298	0.059	0.244	1.160	0.435	-	-	0.095	0.057	**-**	**-**	-	-	4.420
		3	**-4.561**	**0.222**	**0.133**	**0.365**	**1.140**	**0.437**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**4.476**
		4	-3.566	0.289	0.047	0.216	-	-	-	-	-	-	-0.134	0.053	-	-	4.479
	2009	1	-3.360	0.513	0.128	0.357	1.053	0.400	-	-	-	-	**-**	**-**	-0.100	0.050	0

		2	**-4.309**	**0.228**	**0.187**	**0.432**	**1.015**	**0.397**	**-**	**-**	**-**	**-**	-	-	**-**	**-**	**1.763**
		3	-3.114	0.505	0.141	0.375	-	-	-	-	-	-	**-**	**-**	-0.093	0.050	4.684
2009 & 2010	2009	**1**	**-4.534**	**0.164**	**0.047**	**0.217**	**1.312**	**0.360**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**0**
	2010	**1**	**-4.214**	**0.138**	**0.014**	**0.117**	**1.287**	**0.240**	**-**	**-**	**0.096**	**0.032**	**-**	**-**	**-**	**-**	**0**
2008 & 2010	2008	**1**	**-3.374**	**0.233**	**0.114**	**0.338**	**-**	**-**	**-0.069**	**0.021**	**-**	**-**	-	-	**-**	**-**	**0**
	2010	1	-3.595	0.177	0	0	1.124	0.218	-0.045	0.013	0.050	0.026	**-**		-	-	0
		2	**-3.410**	**0.162**	**0.025**	**0.159**	**1.108**	**0.223**	**-0050**	**0.013**	**-**	**-**	**-0200**	**0.057**	**-**	**-**	**0.819**

female neighbour (3/15), density (3/15) and air temperature (2/15). With the exception of the activity of the pup (which was retained in the three confidence sets for 2009 and 2010), no other covariate was retained in the three confidence sets for a given year. The activity of the pup had a positive relationship and was always influential; the distance to the nearest female neighbour and pup age had a negative relationship, and both were always influential. Air temperature and density had a negative and positive relationship, respectively, and both had estimates that were close to, if not less than, twice the standard error. The simplest models for each of the confidence sets are shown in bold in Table 7.4.

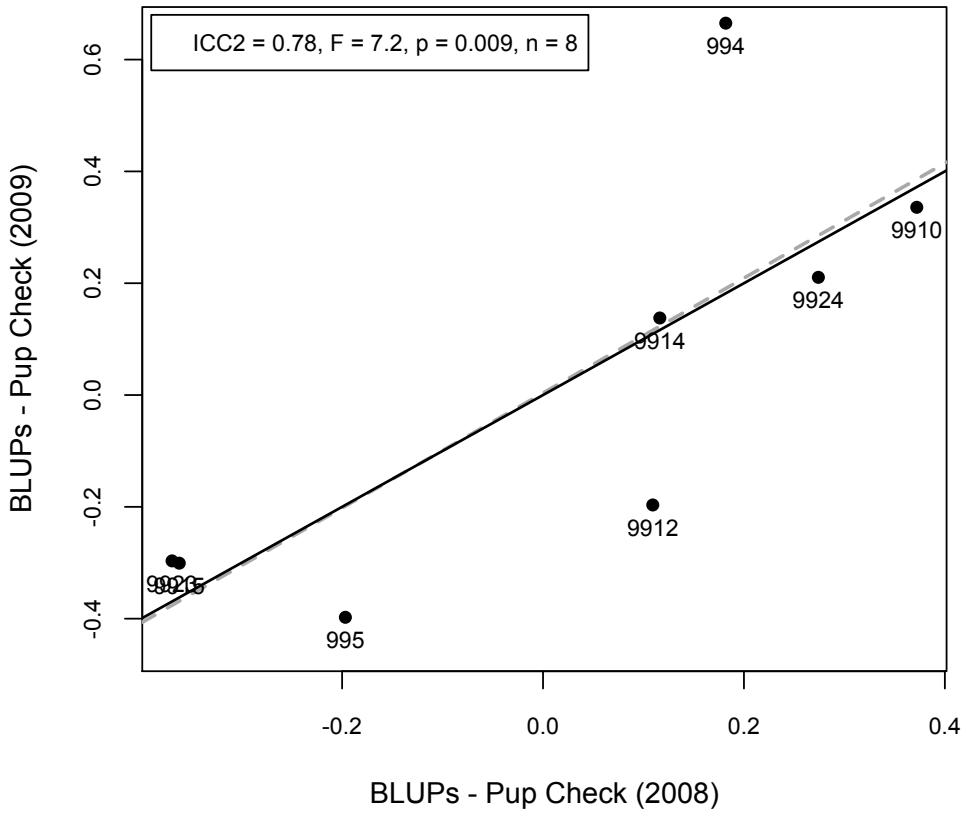


Figure 7.14: The BLUPs extracted from the simplest models for the pup check behavioural category for individuals re-sighted in 2008 & 2009. ICC2 results are shown in the legend within the plot. Individual ID numbers are given for each data point; the line of best fit (black solid line) and the 1:1 line (grey dashed line) are shown. The simplest models are shown in bold in Table 7.4.

Only the BLUPs extracted from the simplest models for the individuals re-sighted in 2008 & 2009 were repeatable (ICC2 = 0.78, F = 7.2, *p* = 0.009; Table 7.5; Figure 7.14). The repeatability estimates for these re-sighted individuals across all possible combinations of the BLUPs extracted from the models retained within the respective confidence sets was variable, with less than half (5/12) the combinations yielding significant estimates (Table A7.25). Of the other three groups of re-sighted individuals, no combination of BLUPs extracted from the models within the respective confidence sets yielded a significant repeatability estimate (Table A7.25).

Table 7.5: ICC2 analyses for the BLUPs extracted from the simplest models for individuals re-sighted in all 3 years (n = 5), 2008 & 2009 (n = 8), 2009 & 2010 (n = 12), 2008 & 2010 (n = 9) for the pup check and alert behavioural categories. All significant results are in bold. Where ICC values are negative the best estimate for repeatability is zero (Hayes & Jenkins, 1997; Bell et al., 2009). The lower and upper columns show the 95% confidence limits.

Behaviour	Years	ICC	F	*p*	lower	upper
Pup Check	2008 – 2010	-0.23	0.55	0.71	-0.59	0.62
	2008 & 2009	**0.78**	**7.2**	**0.009**	**0.18**	**0.95**
	2009 & 2010	-0.19	0.7	0.7	-0.8	0.47
	2008 & 2010	0.24	1.6	0.27	-0.57	0.77
Alert	2008 – 2010	0.36	2.4	0.138	-0.28	0.89
	2008 & 2009	0.18	1.4	0.34	-0.71	0.77
	2009 & 2010	0.4	2.2	0.114	-0.29	0.8
	2008 & 2010	**0.73**	**5.9**	**0.011**	**0.15**	**0.93**

7.4.3.2. Alert

There were 15 models retained across the nine confidence sets for the alert behavioural category. Across all 15 models, the estimated variance of the individuals' ID ranged from 0 to 0.145 (Table 7.6). The activity of the pup was retained in all of the models (15/15), and there was also limited support for pup

Table 7.6: The summary for each of the models that were retained within the confidence set for individuals that were re-sighted in all three years (2008 - 2010; n = 5), 2008 & 2009 (n = 8), 2009 & 2010 (n = 11) and 2008 & 2010 (n = 9) for the **alert behavioural category** (the number of models that were retained at each of the 5 stages of the model selection process is shown in Table A7.24). The models are arranged using the △ value; the AIC value is not presented. If the covariate was retained within the model then the estimated effect (Est.) and the standard error of the estimate (SE) are included in the table. ID was included as a random effect; the variance explained (Var.) and the standard deviation (SD) are included in the table. Models in bold are the simplest model (with the lowest AIC) within the respective confidence set. See the footnote of Table 7.2 for definitions of the covariates. The covariate POOL was not retained in any of the models within the nine confidence sets, and was therefore omitted from the table. The model number (No.) relates to the ICC analyses (Tables A7.26). Table 7.6 is continued overleaf.

					Covariates												
			Intercept		ID		ACT		AGE		DEN		NFN		TEMP		
Analyses	Year	No.	Est.	SE	Var.	SD	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	△
2008 –	2008	1	-2.939	0.263	0	0	1.198	0.299	0.027	0.016	-	-	-0.101	0.028	-	-	0
2010		**2**	**-2.642**	**0.204**	**0.005**	**0.068**	**1.151**	**0.298**	**-**	**-**	**-**	**-**	**-0.104**	**0.029**	**-**	**-**	**0.720**
	2009	**1**	**-2.033**	**0.385**	**0.166**	**0.407**	**1.423**	**0.254**	**-**	**-**	**-**	**-**	**-**	**-**	**-0.117**	**0.033**	**0**
	2010	1	-3.252	0.212	0.099	0.315	1.749	0.225	-0.024	0.014	-	-	-	-	-	-	0
		2	-3.595	0.170	0.041	0.203	1.718	0.222	-	-	0.062	0.033	-	-	-	-	0.246
		3	**-3.448**	**0.174**	**0.088**	**0.296**	**1.757**	**0.224**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**0.999**
2008 &	2008	**1**	**-2.891**	**0.154**	**<0.001**	**<0.001**	**1.351**	**0.230**	**-**	**-**	**-**	**-**	**-0.078**	**0.024**	**-**	**-**	**0**

2009		2	-3.707	0.175	0.016	0.128	1.369	0.232	0.041	0.013	-	-	-	-	-	-	1.549
	2009	**1**	**-2.049**	**0.322**	**0.145**	**0.381**	**1.309**	**0.222**	**-**	**-**	**-**	**-**	**-**	**-**	**-0.112**	**0.029**	**0**
2009 &	2009	1	-3.111	0.130	0.075	0.274	1.252	0.191	-	-	0.038	0.019	-	-	-	-	0
2010		**2**	**-2.982**	**0.116**	**0.085**	**0.292**	**1.204**	**0.189**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**1.963**
	2010	**1**	**-3.232**	**0.120**	**0.097**	**0.312**	**1.688**	**0.167**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**0**
2008 &	2008	**1**	**-3.641**	**0.195**	**0.134**	**0.367**	**1.509**	**0.197**	**0.051**	**0.012**	**-**	**-**	**-**	**-**	**-**	**-**	**0**
2010	2010	1	-3.252	0.148	0.108	0.328	1.372	0.152	-	-	0.057	0.023	-	-	-	-	0
		2	**-3.086**	**0.134**	**0.116**	**0.340**	**1.384**	**0.152**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**3.867**

age (4/15), the distance to the nearest female neighbour (3/15), density (3/15) and air temperature (2/15). With the exception of pup activity (which had a positive, influential relationship with the alert behaviour), the only other covariate that was retained in the three confidence sets for the same breeding season was pup age in 2008. However, across breeding seasons, pup age had both a positive and a negative relationship. Both the distance to the nearest female neighbour and the air temperature had a negative relationship, and were always influential. The influence of the pup age and density was variable (2/4 and 1/3 were considered influential, respectively). The simplest models for each of the confidence sets are shown in bold in Table 7.6.

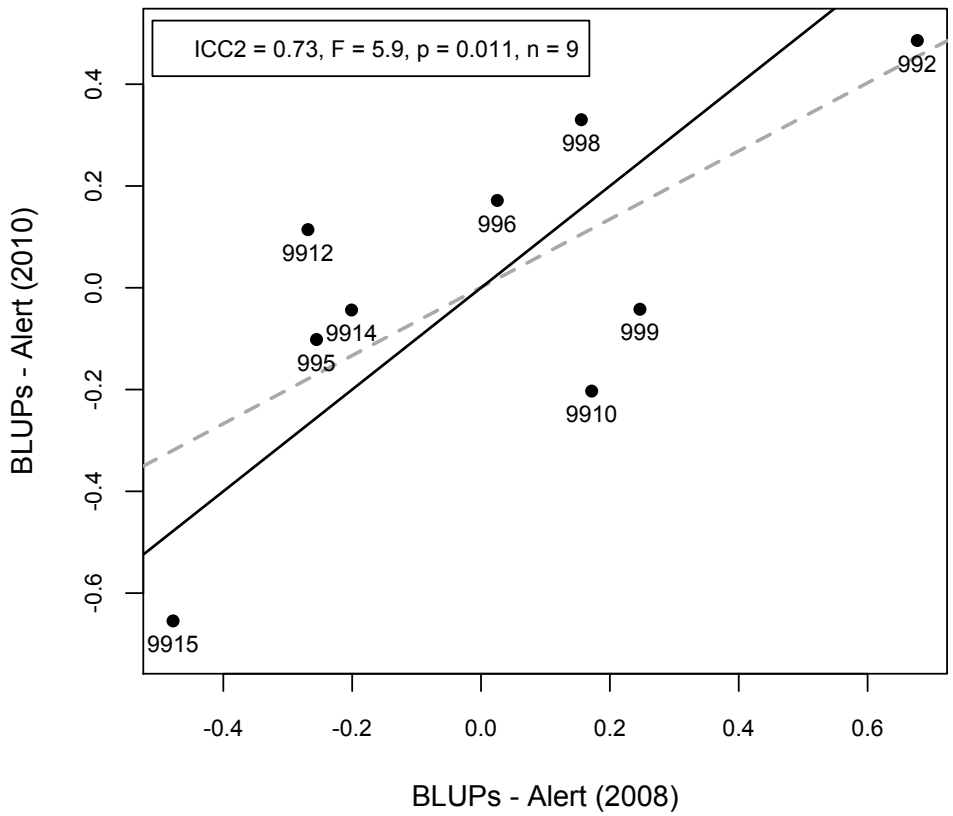


Figure 7.13: The BLUPs extracted from the simplest models for the alert behavioural category for individuals re-sighted in 2008 & 2010. ICC2 results are shown in the legend within the plot. Individual ID numbers are given for each data point; the line of best fit (black solid line) and the 1:1 line (grey dashed line) are shown. The simplest models are shown in bold in Table 7.6.

Only the BLUPs extracted from the simplest models for the individuals re-sighted in 2008 & 2010 were repeatable (ICC2 = 0.73, F = 5.9, p = 0.011; Table 7.5; Figure 7.13). Nevertheless, the repeatability estimates for these re-sighted individuals were robust to all possible combinations of the BLUPs extracted from the models retained within the respective confidence sets (Table A7.26). Of the other three groups of re-sighted individuals, no combination of BLUPs extracted from the models within the respective confidence sets yielded a significant repeatability estimate (Table A7.26).

7.5. Discussion

Based on previous studies (Twiss & Franklin, 2010; Twiss et al., 2011a), and the results presented in Chapters 4, 5 and 6, only the pup check and the alert behavioural categories shall be discussed herein. Furthermore, as the gross activity budgets for these behavioural categories were not significantly different between the two study sites, it is possible to make direct comparisons between the results from the SA and the NSA analyses. The initial sections of the discussion shall compare the findings at each step of the analyses and, where possible, shall provide a biological interpretation of the models retained within the confidence sets for each of the behavioural categories. These shall be discussed in relation to previous studies and the results of the NSA analyses presented in the previous three chapters of this thesis. Thereafter, the differences between the SA and the NSA shall be discussed, with respect to which, if any, of the deviations from the NSA data collection protocol, may have had an influence on the outcome of these results.

7.5.1. Pup check

The pup check behavioural category was not robustly repeatable at any step of the analyses. Both steps 1 and 3 found that the individuals re-sighted in 2008 & 2009 were repeatable; however, step 2 did not retain individuals' ID in the 2008 confidence set for this group of re-sighted individuals. Despite this, the continuous covariates retained in the respective confidence sets for step 2 (GLMs) and step 3 (GLMMs), were very similar. Similarly, for the NSA data, this behaviour

was not robustly repeatable. However, where behaviour was repeatable in steps 1 and 3, the individuals' ID was retained within the respective models in step 2. Therefore, the pattern in the results for the three-step analyses between the two study sites did vary, albeit slightly.

7.5.2. Alert

In the first step of the analyses, the alert behaviour for three of the four groups of re-sighted individuals yielded a significant repeatability estimate. In the second step, individuals' ID was retained in 8 of the 9 confidence sets. These two steps did complement one another, such that the 2008 & 2009 re-sighted individuals' dataset was not repeatable in step 1, and individuals' ID was not retained in any of the 2008 models using the 2008 & 2009 re-sighted individuals' dataset in step 2. However, in step 3 only one of the three groups of re-sighted individuals remained repeatable. Despite this, the continuous covariates retained in the respective confidence sets for step 2 (GLMs) and step 3 (GLMMs), were very similar. In comparison, the alert behaviour was repeatable in steps 1 and 2 for all four groups of re-sighted individuals in the NSA, and in step 2, individuals' ID was retained within all of the models. Therefore, the general patterns in the results for steps 1 and 2 were similar between the two sites, but for step 3, the pattern was not maintained in the SA. The reasons for these variations in both the pup check and the alert behaviours between the two sites shall be discussed later, in Section 7.5.5.

7.5.3. General patterns in the models

Some of the results for the pup check and the alert behavioural categories were similar. To avoid repetition, they shall both be discussed in this section. With the exception of the activity of the pup, there was little support for any one covariate within, or between confidence sets. Therefore, there was no consistency with respect to which of the covariates were influential across re-sighted individuals' datasets and/or across breeding seasons. Furthermore, collinear covariates were often retained within competing models, and at least one covariate retained within multiple confidence sets had a positive and a negative

influence across breeding seasons, which suggests that the collinear covariates that were omitted may (also) have been influencing behaviour.

The influence of smaller sample sizes was also evident in the SA data. For example, where the activity of the pup was retained, greater proportions of pup activity generally had fewer observed data. Consequently, the 95% confidence intervals for the observed and fitted data were considerably wider when the proportion of time the pup spent active was ca. ≥ 0.6. This could be because pups are rarely active for such high proportions of time; therefore, the model would be expected to perform poorly at higher proportions of pup activity. For pup age, the sample size cannot be explained as a function of the biology or ecology of the individuals. Therefore, the same patterns seen in these data (as a result of smaller sample sizes, which could have theoretically been avoided) could be an indication that there were too few data, and, as a result, the model failed to fit these data. Consequently, considering pup age when making inference on the covariates that best explain variation in behaviour, is likely to lead to erroneous conclusions (see below).

Given that the covariates retained within and between confidence sets varied considerably (which was, in part, influenced by collinearity), and that some models failed to fit the observed data for some influential covariates, it is difficult to biologically interpret the models more generally across groups of re-sighted individuals and/or across breeding seasons. Notably, the activity of the pup (where retained) always had a positive relationship; for the pup check behaviour, this covariate was retained in the majority of the models and was almost always influential; and for the alert behaviour, it was retained in all of the models and was always influential. Therefore, the more active the pup was, the more time the mother spent pup checking and alert, which does make biological sense (Fogdon, 1971; Kovacs, 1987; Smiseth & Lorentsen, 1995a, b, Chapter 5, Section 5.5.1 and Chapter 6, Section 6.6.1). The results of the NSA analyses also showed a similar pattern; the activity of the pup had a positive relationship with both behaviours, and was retained in all of the pup check models and the majority of the alert models, and where retained it was always influential (Chapter 5, Sections 5.4.2 and 5.4.3 and Chapter 6, Sections 6.5.2 and 6.5.3). Therefore, the results from the

SA and the NSA provide strong evidence, which suggests that the activity of the pup does have a considerable influence on the proportion of time a mother spends pup checking and alert.

7.5.4. Previous studies on the repeatability of wild grey seals' behaviour

During the 2009 breeding season, Twiss et al. (2011a) used in-field behavioural tests to show that the pup check behaviour of females in the SA was highly repeatable within a breeding season (ICC2 = 0.80, $p \leq 0.001$, n = 20). Furthermore, the preliminary analysis of data collected during the 2010 breeding season (using the same methodology) has also yielded a high repeatability estimate within and across (the 2009 and 2010) breeding seasons (Twiss et al., unpublished data). Therefore, this approach for identifying CIDs in the pup checking behaviour does appear to be robust. However, the pup itself is likely to be an important covariate, which should be considered when comparing within breeding seasons (where the pup is the same individual) and across breeding seasons (where the pup is a different individual). Assuming that individual variation in behaviour occurs in pups, and knowing (from previous studies and the results presented in this, and previous chapters) that females do react to their pups' behaviour (Fogdon, 1971; Kovacs, 1987; Smiseth & Lorensten, 2001), then the pup may have a substantial influence on whether or not their mothers behaviour is repeatable across breeding seasons. Conversely, within breeding seasons, this potentially influential covariate is controlled for. Furthermore, behaviour manipulated during in-field experiments may not be representative of the same behaviour elicited under 'natural conditions' (Twiss et al., 2011b; Chapter 1, Section 1.6). Therefore, it is important to consider whether or not a novel (and indeed, a non-novel) behavioural test is likely to result in an ecologically meaningful conclusion.

Using data collected during the 1988 and 1989 breeding seasons, Twiss & Franklin (2010) showed that the alert behaviour of male grey seals in the SA was highly repeatable across two breeding seasons (ICC2 = 0.83, $p = 0.002$, n = 8). Similar to the present study, they attempted to 'explain away' the repeatability of behaviour. They used data obtained from observations and from catching and

handling, to assess whether or not repeatability was influenced by: 1) state dependent factors (such as body size, mass, or mass loss rate), 2) age, 3) colony attendance patterns (such as length of stay, arrival or departure days), 4) home range size, 5) rates of sexual or aggressive interactions, 6) dominance rank, 7) within season mating success, or 8) reproductive longevity. They found that none of these factors showed a consistent relationship with the repeatability of the alert behaviour, concluding that the CIDs in the alert behaviour were independent of short- or long-term fitness consequences. In the present study, social and environmental covariates were used to 'explain away' the repeatability of the alert behaviour in female grey seals. For the SA, the repeatability of the alert behaviour was not robust to the inclusion of these covariates. However, the same was not true for the NSA analyses, where the alert behaviour remained robust and highly repeatable, despite the influence of these social and environmental covariates. Potential reasons for the variation in the results between the SA and the NSA, along with the use of short- and long-term proxies of fitness for quantifying CIDs in behaviour, shall be discussed in greater detail, below.

7.5.5. The potentially influential differences between the NSA and the SA

There are several reasons why the patterns observed across the three-step analytical process differed between the NSA and the SA for the pup check and the alert behaviours, these are listed below and each shall be discussed in turn:

1) Individual variation and the influence of sample size.
2) Temporal variation in collection of the behavioural data.
3) Temporal variation in collection of the spatial data.
4) The importance of a temporally suitable pool coverage.
5) The omission of potentially influential covariates.
6) The capturing and handling of individuals.

Points 1 - 5 will be discussed briefly, and shall be revisited in Chapter 9 where a more comprehensive account of the methodological considerations that have been raised in this, and previous chapters, shall be discussed.

7.5.5.1. Individual variation and the influence of sample size

A visual comparison of the SA and the NSA plots for step 2 of the analyses shows that there was typically more within-individual, and less between-individual variation in the SA females for both behavioural categories (SA: Chapter 6, Sections 6.5.2 and 6.5.3; NSA: Chapter 5, Sections 5.4.2 and 5.4.3). The range of the between-individual variation in the alert behaviour was comparable for the groups of re-sighted individuals' between the two study sites. However, for the pup check behaviour the between-individual variation in the SA females was approximately half that of the NSA. In both the SA and the NSA re-sighted individuals' datasets, there were certain individuals that heavily influenced whether or not individuals' ID was retained in the models. This was particularly true for the pup check behaviour for the NSA datasets, and for both behaviours for the SA datasets. Therefore, in these instances, whether or not individuals' ID was retained within a confidence set in step 2 of the analyses was dependent upon which individuals were included in the analyses. Furthermore, across breeding seasons, some individuals' behaviour may be more (or less) consistent than others (Hayes & Jenkins, 1997; Bell et al., 2009), which could have a considerable influence on the repeatability estimates in steps 1 and 3. Consequently, the individuals that were included from the wider population will heavily influence all three steps of the analyses for both study sites.

7.5.5.2. Temporal variation in collection of the behavioural data

The behavioural data from the NSA were collected on most days during daylight hours (Chapter 2, Section 2.5.4), whereas the behavioural data from the SA were collected intermittently, which typically resulted in several days of missing data for each of the individuals (Tables A7.1 - A7.3). This was particularly true for the beginning of lactation, where only one of the individuals was observed for all three of the first days postpartum (i.e. the first lactation period; Chapter 3, Sections 3.6 and 3.8.2). The exploratory analysis of the NSA data showed that there were significant differences in five of the eight behavioural categories across the three lactation periods (Chapter 3, Section 3.6). Consequently, the intermittent approach to data collection, coupled with the shorter duration of the first and third lactation

periods, may mean that important variation in an individual's behaviour was missed, which, could in turn, reduce the likelihood of identifying CIDs in certain behaviours.

7.5.5.3. Temporal variation in collection of the spatial data

Given that the maximum number of data points for each of the spatial covariates per individual did not exceed 16, the spatial data for the SA may not provide an accurate representation of the social and environmental variation that an individual experiences whilst on the breeding colony. Furthermore, as a result of the small sample sizes, it was not possible to calculate accurate kernel density estimates. In addition to these issues, the temporal scale at which the spatial data were collected may have been too coarse, given that the behavioural data were analysed as hourly activity budgets. Consequently, only one map location per day was used to explain the variance in behaviour over several hours, which may explain why the spatial covariates were infrequently retained within the confidence sets.

7.5.5.4. The importance of a temporally suitable pool coverage

The distance to the nearest pool was calculated using a pool coverage from the 1994 breeding season, which may not have been fully representative of the distribution of pools in 2008, 2009 and 2010. The exploratory analyses of the NSA data showed that in a 'typical' breeding season (with respect to the weather conditions; Chapter 3, Section 3.14), the distance to the nearest pool had a positive relationship with density and rainfall, and a negative relationship with the distance to the nearest female neighbour and air temperature. Across the nine re-sighted individuals' datasets for the SA, the distance to the nearest pool was significantly collinear with one or more of these covariates. However, where a significant correlation did occur, these relationships were not always consistent. This may be explained by the fact that females in the SA are closer to pools of water than their counterparts in the NSA (as was shown in the exploratory analyses). Consequently, the influence of the weather parameters on the distance

to the nearest pool, and in turn, density and the distance to the nearest female neighbour would be greatly reduced.

7.5.5.5. The omission of potentially influential covariates

The home range usage, the distance to the pup and the amount of rainfall were all omitted from the SA analyses due to insufficient data. The exploratory analyses of the NSA data showed that these three covariates did influence behaviour on the colony (Chapter 3, Section 3.14). Furthermore, the results of the in-depth collinearity analyses of the NSA data were critically important for building hypotheses and for making inference on the resulting confidence sets of models. It was assumed that the same relationships between covariates existed in the SA, which meant that covariates that were not collected (e.g. distance to the pup), were nonetheless represented by (what were assumed to be) collinear covariates (i.e. distance to the nearest pool). However, as noted in Section 7.5.5.4 above, the exploratory analyses of the SA data suggested that this might not have been the case.

In step 3 of the analyses, it is important to reiterate that the BLUP represents the variation for individual *x*, which has not been captured by the explanatory covariates included in the model (Pinheiro & Bates, 2000; Kruuk, 2004; Crawley, 2007; Everitt & Hothorn, 2011). Therefore, by omitting influential covariates from the analyses, the variance that would have otherwise been explained by these covariates is captured by individuals' ID. Consequently, this would influence the BLUPs, which in turn would influence the repeatability estimates. Therefore, this may explain why the repeatability of the alert behaviour for the SA datasets was not as robustly repeatable in step 3, as it was in step 1. Furthermore, it also supports the supposition that influential covariates may have been omitted from the SA analyses (or may not have been collected at an adequate temporal resolution).

7.5.5.6. Capturing and handling of individuals

Behavioural observations were not undertaken on catching days; therefore, between catching and handling there would have been a minimum duration of ca. 16 hours prior to behavioural observations. Nevertheless, studies in other species have shown that capturing and handling individuals can affect both short- and long-term behaviour (Pedersen, 1994; Andrade et al., 2001; Ellenburg et al., 2009; Hogan et al., 2011). With respect to pinnipeds, the majority of studies are interested in the effects of capturing and handling on the probability of survival into the following breeding season (e.g. Baker & Johanos, 2002; McMahon et al., 2005). There are some studies that have addressed short-term effects, but these are typically physiological rather than behavioural (e.g. Engelhard et al., 2002; Harcourt et al., 2010). The short-term effects of capturing and handling on behaviour could be quantified by comparing behavioural observations at set intervals prior to, and post capture. If behaviour were significantly different, then it would be possible to estimate how long it takes for an individual's behaviour to return to 'normal', which could then be factored into these analyses.

7.6. Conclusions

Using data collected in the SA, the three-step analytical approach did identify CIDs in the pup check and the alert behaviours of postpartum female grey seals. The patterns in the results across the three steps were not as robust for the SA data as they were for the NSA data; this was particularly true for step 3 of the analyses for the alert behavioural category. There were a number of deviations from the NSA sampling protocol, all of which were briefly discussed; however, it was not possible to state which (if any) of these had the greater influence on the repeatability estimates. Nevertheless, these findings do illustrate the importance of including all potentially influential covariates in a model; and they also illustrate the importance of recording covariates at a temporal scale that is suitable for the analyses intended. A potential approach for identifying which of the deviations from the NSA sampling protocol was the most influential, shall be given in the general discussion (Chapter 9), along with suggestions for optimising the likelihood of identifying CIDs in the behaviour of wild animals in the field.

Chapter Eight:
Do individual differences in behaviour correlate with short-term fitness proxies?

8.1. Introduction

Long-term, longitudinal studies of female grey seal reproduction on North Rona have provided substantial evidence for the importance of individual variation in reproductive output. Using 16 years of data, Pomeroy et al. (1999) found that females with a greater maternal mass at parturition produced heavier pups at weaning and tended to give birth earlier in the season. They also found that individual, which was included in a generalised linear model (GLM) as a fixed-effect, explained 75% of the variation in the weaning mass of pups, despite the influence of other covariates (such as maternal mass at birth, duration of lactation, maternal length, year, pup sex, date of birth and mass of pup at birth). Furthermore, 57% of the females included in the study produced 74% of the pups that were raised successfully to weaning. Therefore, by using several proxies of short-term fitness, Pomeroy et al. (1999) showed that there was more variance in the reproductive performance between mothers than expected.

In their analyses, Pomeroy et al. (1999) also found that almost half of the variation in pup mass at weaning was explained by the year in which the pup was born (48.9%). They suggested that a reduced efficiency of mass transfer in some years may have occurred as a result of environmental variation (e.g. air temperature and rainfall), changes in social structure on the breeding colony and/or individual variation in behaviour. More recently, studies have shown that variation in the environment does influence maternal behaviour on the breeding colony (Redman et al., 2001; Twiss et al., 2002); that specific females do form active associations (Pomeroy et al., 2005); and that the plasticity of certain aspects of females' behaviour may be constrained (Twiss et al., 2011a; Chapters 4, 5, 6 and 7). Therefore, as suggested by Pomeroy et al., (1999), some of the variance explained by individuals' identity and year, may have otherwise been explained by influential covariates that were not included in their models.

8.2. Aims

The data analysed in this chapter were collected in the study area (SA) on North Rona (Chapter 2, Section 2.3 and Chapter 7, Section 7.3.1), during the 2008 and 2009 breeding seasons. These data included behavioural observations and reproductive measures, which are taken routinely, as part of the long-term longitudinal studies of postpartum females on North Rona (Chapter 2, Section 2.3.1). The principal aim of this chapter is to determine whether or not individuals' behaviour explained any of the variation in the pup daily growth rate and/or the mother-pup mass transfer efficiency (Section 8.3) despite including other covariates in the analyses, which are known to influence the pup mass at weaning (Pomeroy et al., 1999). The findings presented here shall be compared with those from previous studies on maternal investment in pinnipeds. The potential influence of consistent individual differences (CIDs) in behaviour (Chapters 4, 5, 6 and 7) on these commonly used proxies for short-term fitness shall also be considered.

8.3. Methods

During the 2008 and 2009 breeding seasons, Dr. Paddy Pomeroy (PPP) collected reproductive data on postpartum females, these data included the: 1) pups' daily growth rate (kg; PDGR), 2) mother-pup mass transfer efficiency (%; MTE, calculated as the % of maternal mass loss gained by pups over an interval, usually ≥ 10 days), 3) maternal postpartum mass (kg; MPPM), 4) mothers' daily mass loss (kg; MDML), 5) duration of lactation (number of days; DURLACT), 6) date of parturition (DOB), 7) pup sex 8) age of the mother (years). These eight measures shall be referred to as 'reproductive' variables throughout this chapter. See Pomeroy et al. (1999) for full details on how the females were captured and handled, and how each of these variables was derived from the metrics collected. For each of the reproductive variables, there was one data point for each individual, for each breeding season.

Using five minute scan samples and following the ethogram presented in Chapter 2, Section 2.5.3, Dr. Sean Twiss (SDT) collected the behavioural data for all of the individuals captured and handled by PPP (see Chapter 7, Section 7.3.1,

for more information on the behavioural observations). Only individuals that were included in the gross dataset after omitting outliers (Chapter 7, Appendix, Section A) were included in the analyses presented in this chapter. Of these individuals, there were a total of 29 that had reproductive data (14 and 15 individuals in the 2008 and 2009 breeding seasons, respectively; 8 of these individuals were re-sighted in both breeding seasons). The behavioural data for each of the individuals were extracted from their gross activity budget (Chapter 7, Section 7.3.2). Therefore, for each of the eight behavioural categories there was one data point for each individual, for each breeding season.

As noted in Section 8.1, Pomeroy et al. (1999) found a considerable year effect on pup weaning mass within mothers, even after accounting for potentially influential covariates (MPPM, DURLACT, and maternal length). Consequently, in the present study, each breeding season shall be analysed separately. There was no formal treatment of pup sex in the analyses because the data were skewed (2008: 9 male and 5 female pups; 2009: 6 male and 9 female pups). However, to allow for a qualitative assessment, the sex of the mothers' pup shall be shown in all figures presented in this chapter. The age of 13 of the 29 females was known (which ranged from 15 to 27 years old). As a result of the small sample size, mother's age was not included in the analyses; however, to allow for a qualitative assessment, the age of the mothers (where known) shall be provided in the figure legends.

In two separate analyses, the PDGR and the MTE were included as response variables in a linear model. For both of these analyses, the MDML, MPPM, DURLACT, DOB and one of the eight behavioural categories were included as explanatory variables. Each of the eight behavioural categories were analysed separately; therefore, for each response variable there were 8 confidence sets. Model selection was made using AICc (Chapter 5, Appendix, Section B) and was carried out using the process detailed in Chapter 5, Section 5.3.6; therefore, it shall not be reiterated here. Covariates retained in the linear models were considered influential if they had an estimate that was greater than twice the standard error (Crawley, 2007). For each of the confidence sets, the observed values were plotted against the fitted values for the simplest model with

the lowest AICc. Only covariates that were influential were plotted. The behavioural covariates were plotted if they were retained in any of the models within the confidence set and were influential (irrespective of whether or not they were retained within the simplest model with the lowest AICc). Prior to modelling the data, the Spearman's rank correlation coefficient was used to test for collinearity between each of the explanatory variables, and for any relationship between the response and explanatory variables (Zuur et al., 2009a). All significant correlations ($p < 0.05$) were plotted and the results of the Spearman's rank correlation coefficient are shown in the legend. In all of the figures presented in this chapter, the individual ID numbers are given for each data point (Chapter 7, Section 7.3.6); black data points = male pups, grey data points = female pups. The black solid line shows the line of best fit.

8.4. Results

For both breeding seasons, the Spearman's rank correlation coefficient showed that: heavier females produced heavier pups (Tables 8.1a and 8.1b; Figure 8.1); heavier females lost more mass per day (Figure 8.2); and heavier females had a longer duration of lactation (Figure 8.3). In 2008, pup daily growth rate increased with an increase in mothers' daily mass loss (Table 8.1a and Figure 8.4a) and although not significant, there was a similar pattern in 2009 (Figure 8.4b). There was also a significant, negative correlation between mothers' daily mass loss and mass transfer efficiency in 2009 (Table 8.1b and Figure 8.5b); however, these data were widespread, and there was no evidence from the 2008 breeding seasons that this pattern was consistent across the two breeding seasons (Table 8.1a and Figure 8.5a)

Table 8.1: The results of the Spearman's rank correlation coefficient analyses comparing each of the reproductive variables for the **a)** 2008 and **b)** 2009 breeding seasons for all individuals (N = 14 and 15, respectively). The *p* value is given above, and the r value below; significant results are in bold. See Section 8.3, for the full definition of each of the reproductive variables.

a)

	PDGR	MTE	MPPM	MDML	DURLACT	DOB
PDGR		0.204 0.361	**0.026** **0.6**	**<0.001** **0.785**	0.059 0.517	0.791 0.078
MTE			0.365 0.262	0.472 -0.209	0.094 0.464	0.744 -0.1
MPPM				**0.04** **0.554**	**0.03** **0.579**	0.113 0.443
MDML					0.337 0.277	0.319 0.287
DURLACT						0.476 0.208
DOB						

b)

	PDGR	MTE	MPPM	MDML	DURLACT	DOB
PDGR		0.386 0.242	**0.01** **0.657**	0.076 0.475	0.187 0.36	0.292 -0.292
MTE			0.718 -0.102	**0.007** **-0.662**	0.995 0.002	0.347 0.262
MPPM				**0.019** **0.607**	**0.011** **0.636**	0.914 0.031
MDML					0.631 0.135	0.401 -0.234
DURLACT						0.914 0.031
DOB						

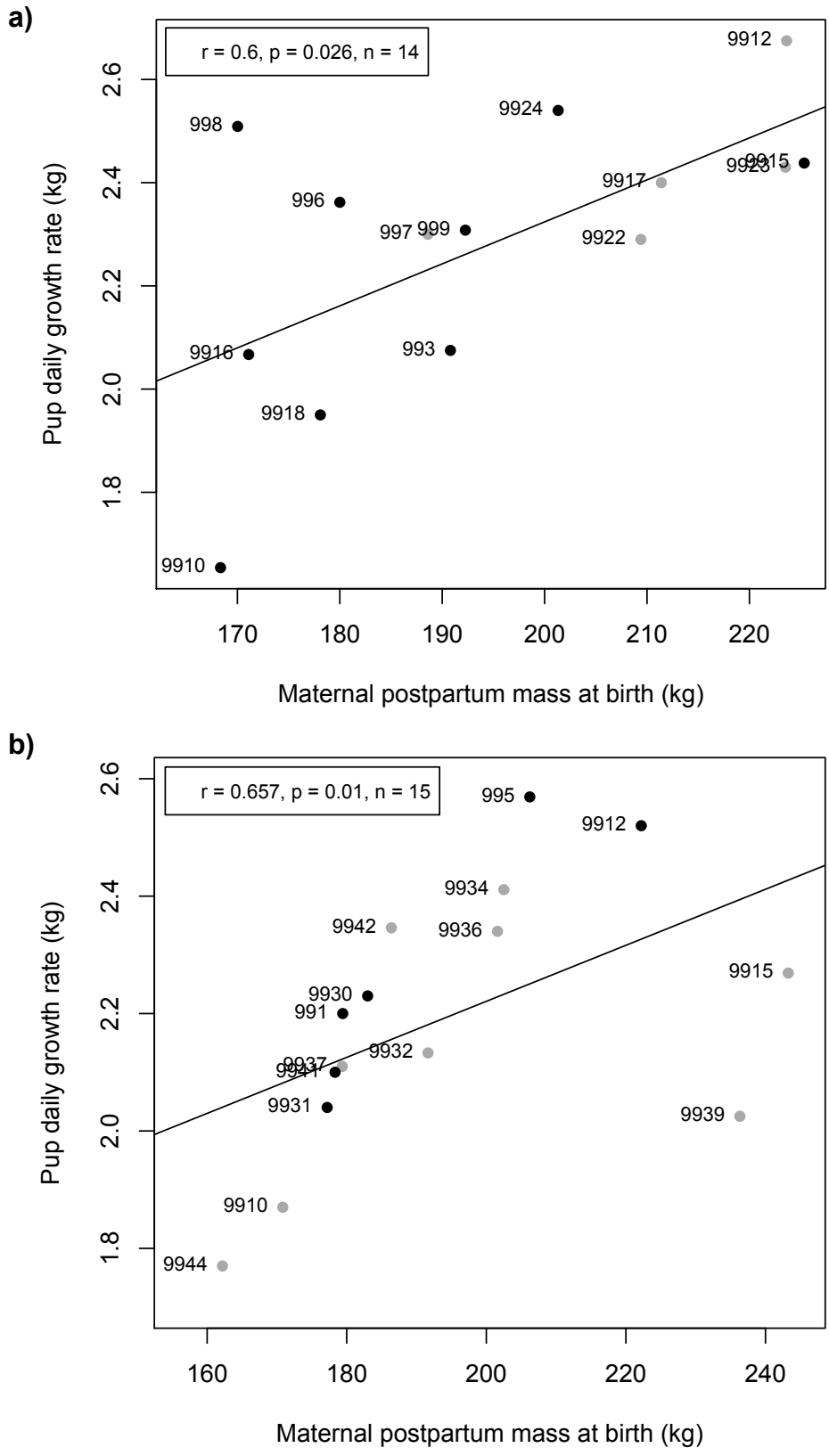


Figure 8.1: The maternal postpartum mass at birth (kg) plotted against the pup daily growth rate (kg) for the **a)** 2008 and **b)** 2009 breeding seasons. The age (in years) of these females were **a)** ID994 = 23, ID996 = 17, ID997 = 15, ID998 = 18, ID9912 = 21, ID9915 = 17, ID9924 = 22. The age of the other 7 individuals is not known and **b)** ID995 = 27, ID9912 = 22, ID9915 = 18, ID9942 = 20. The age of the other 11 individuals is not known.

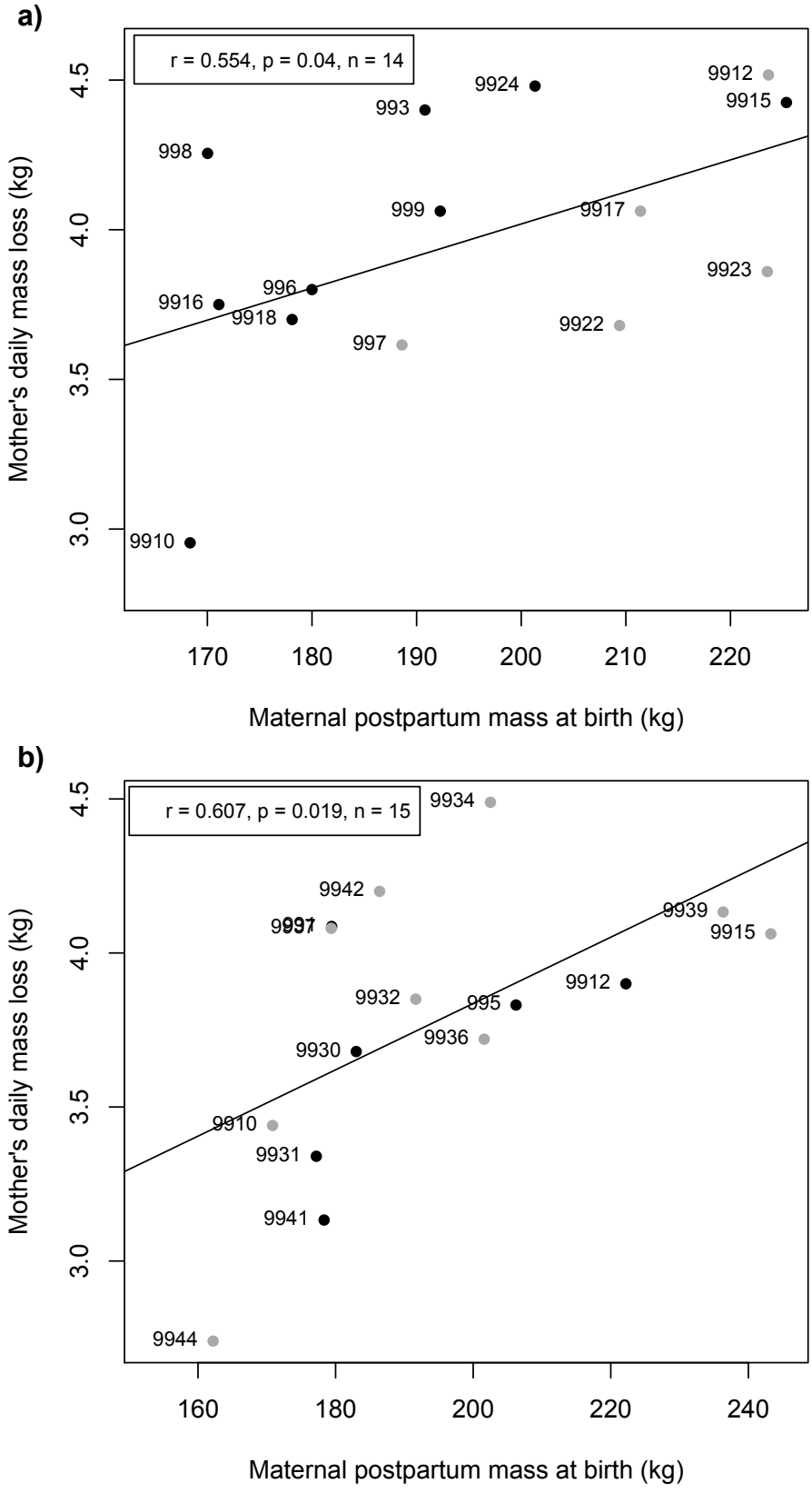


Figure 8.2: The maternal postpartum mass at birth (kg) plotted against the mother's daily mass loss (kg) for the **a)** 2008 and **b)** 2009 breeding seasons. The age (in years) of these females are shown in the legend for Figure 8.1.

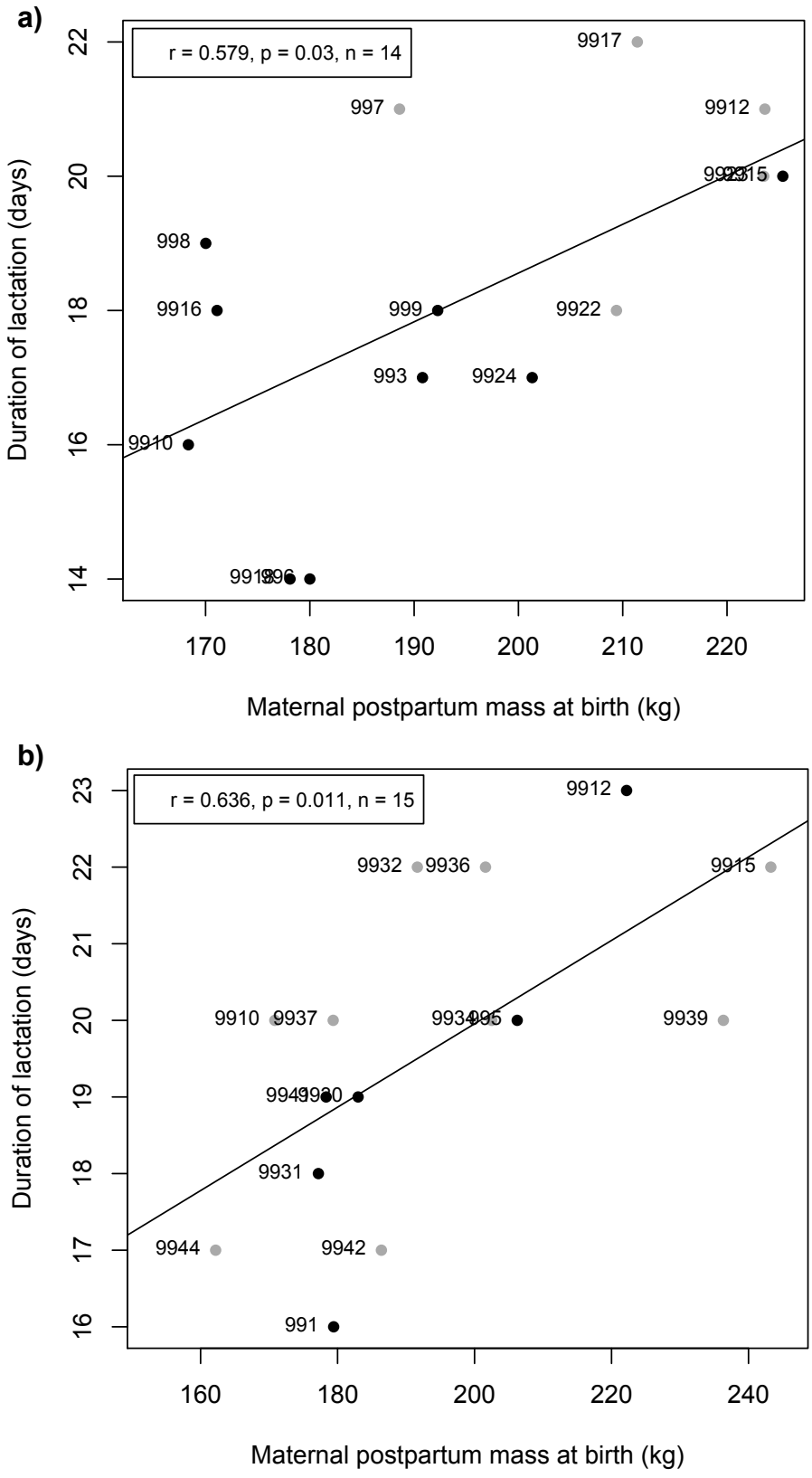


Figure 8.3: The maternal postpartum mass at birth (kg) plotted against the duration of lactation (days) for the **a)** 2008 and **b)** 2009 breeding seasons. The age (in years) of these females are shown in the legend for Figure 8.1.

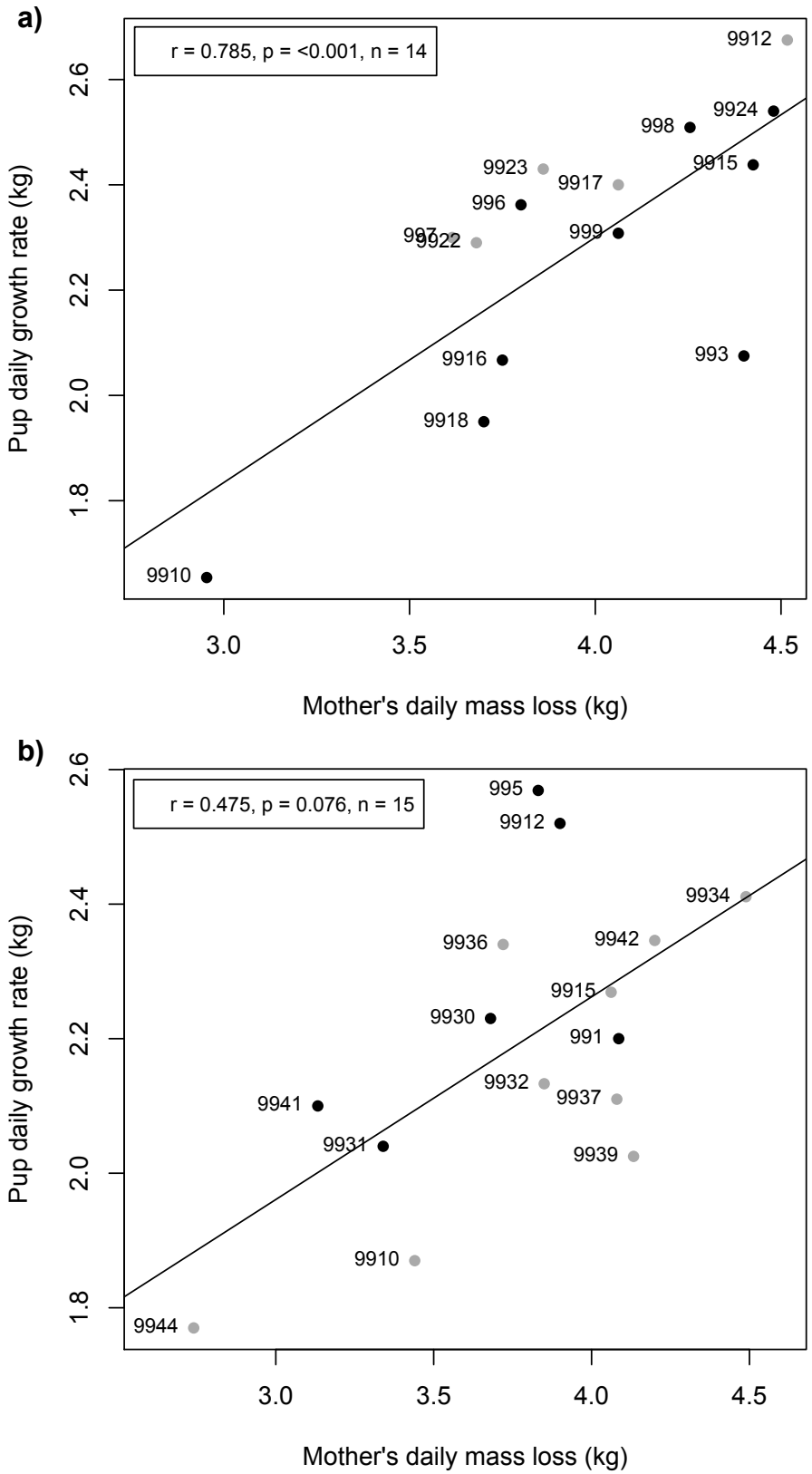


Figure 8.4: The mother's daily mass loss (kg) plotted against the pup daily growth rate (kg) for the **a)** 2008 and **b)** 2009 breeding seasons. The age (in years) of these females are shown in the legend for Figure 8.1.

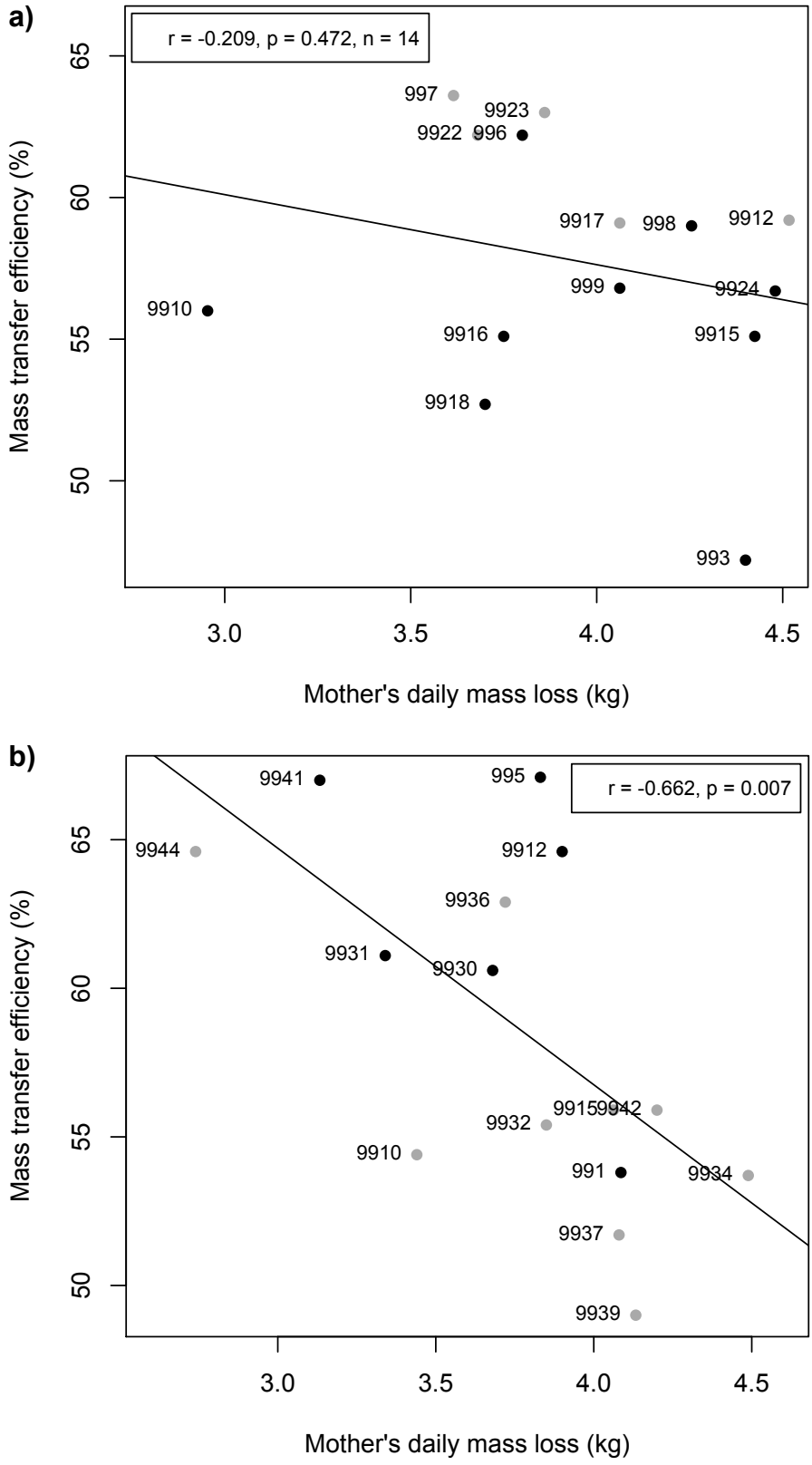


Figure 8.5: The mother's daily mass loss (kg) plotted against the mass transfer efficiency (%) for the **a)** 2008 and **b)** 2009 breeding season. The age (in years) of these females are shown in the legend for Figure 8.1.

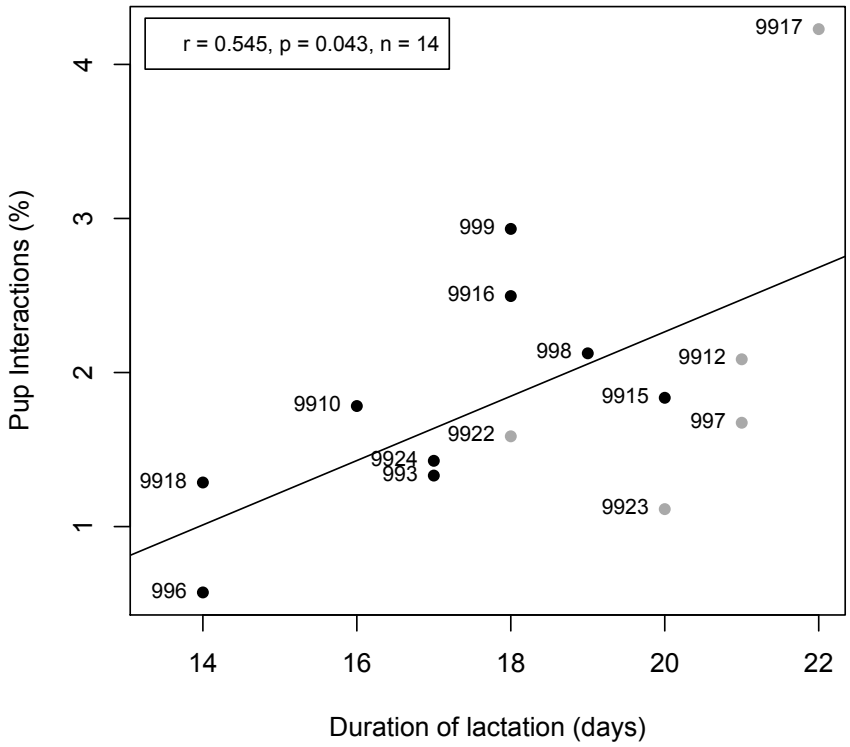


Figure 8.6: The duration of lactation (days) plotted against the percentage of time spent in the pup interaction behavioural category for the females seen in the 2008 breeding season. The age (in years) of these females are shown in the legend for Figure 8.1.

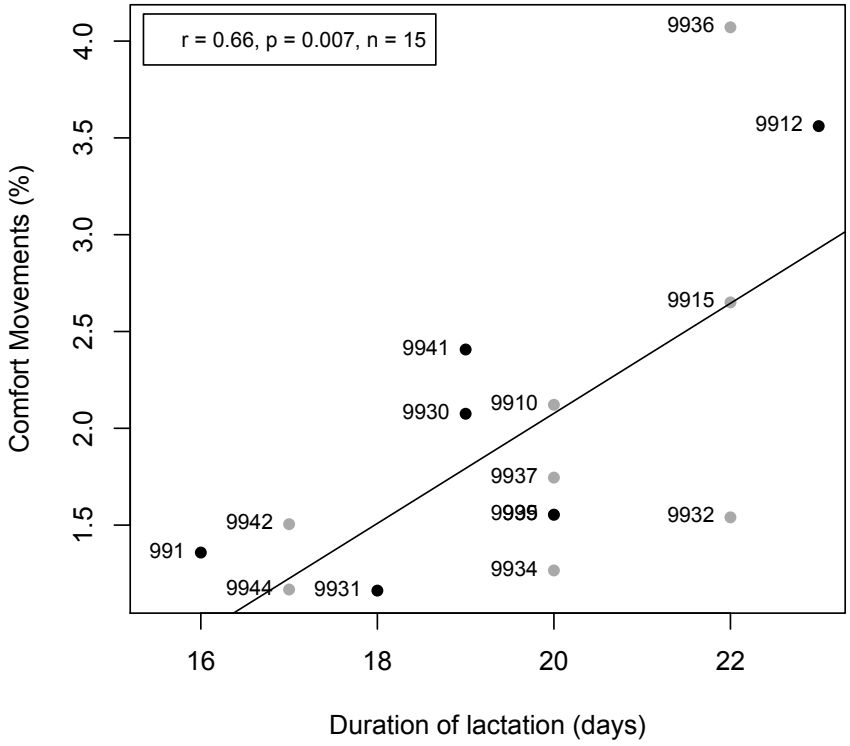


Figure 8.7: The duration of lactation (days) plotted against the percentage of time spent in the comfort movement behavioural category for the females seen in the 2009 breeding season. The age (in years) of these females are shown in the legend for Figure 8.1.

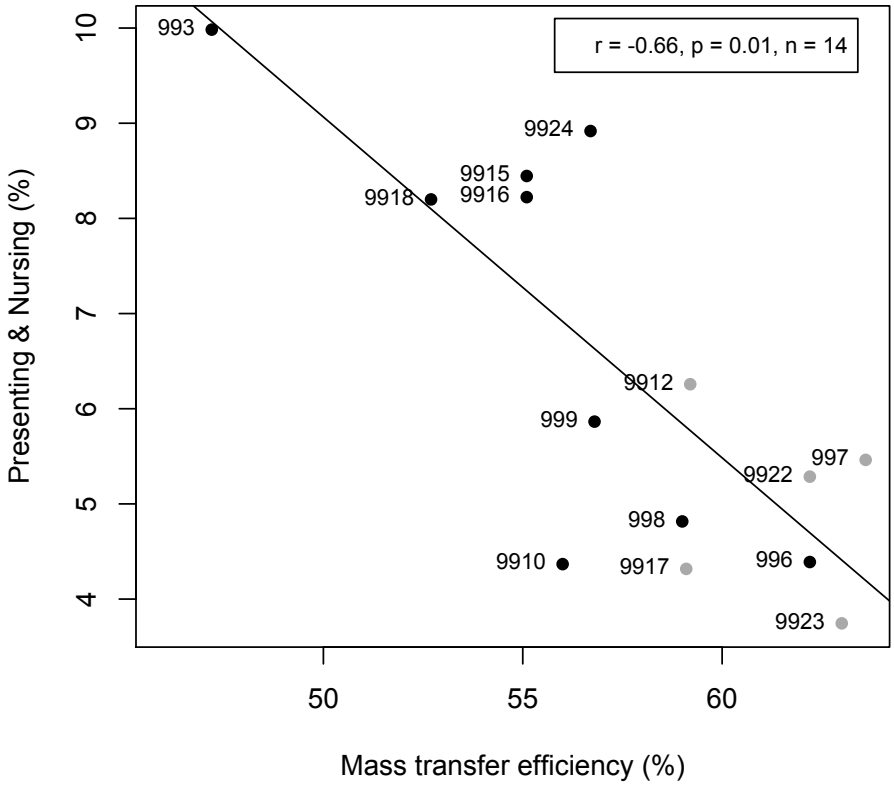


Figure 8.8: The mass transfer efficiency (%) plotted against the percentage of time spent in the presenting & nursing behavioural category plotted for the females seen in the 2008 breeding season. The age (in years) of these females are shown in the legend for Figure 8.1.

There was little evidence to suggest that behaviour was correlated with any of the reproductive variables, and where correlations did occur, they were not consistent across breeding seasons (Table 8.2). Of those that were significant, the pup interactions (2008; Figure 8.6) and the comfort movement (2009; Figure 8.7) behavioural categories were positively collinear with duration of lactation (r = 0.545, p = 0.043; r = 0.66, p = 0.007, respectively), and the presenting & nursing behavioural category (2008; Figure 8.8) was negatively collinear with mass transfer efficiency (r = -0.661, p = 0.001). Despite collinearity in some of the reproductive and behavioural covariates, all covariates were included in the linear models. Consequently, collinearity shall be dealt with as part of the model selection process (see Chapter 5, Section 5.3.6).

Table 8.2: The results of the Spearman's rank correlation coefficient analyses comparing each of the behavioural categories with th two response and the four reproductive explanatory variables for the 2008 and 2009 breeding seasons for all individuals (N = 14 and 15, respectively). The *p* value is given above, and the r value below; significant results are in bold and marked with an *. See Section 8.3 for the full definition of each of the reproductive variables.

	2008						2009					
Behaviour	Response		Explanatory				Response		Explanatory			
	PDGR	MTE	MPM	MDML	DURLACT	DOB	PDGR	MTE	MPM	MDML	DURLACT	DOB
Resting	0.638	0.081	0.532	0.459	0.786	0.916	0.883	0.259	0.397	0.354	0.654	0.42
	0.138	0.482	0.182	-0.216	-0.08	-0.031	-0.043	-0.311	0.236	0.257	0.126	0.225
Comfort	0.797	0.229	0.522	0.631	0.354	0.958	0.32	0.375	0.182	0.667	**0.007***	0.779
movement	0.077	-0.344	-0.187	0.141	-0.268	0.016	0.275	0.247	0.364	-0.121	**0.66**	0.079
Pup	0.892	0.463	0.295	0.333	0.549	0.224	0.289	0.419	0.307	0.812	0.409	0.512
check	-0.042	0.214	-0.301	-0.279	0.175	-0.347	-0.293	-0.225	-0.282	-0.068	-0.23	-0.184
Alert	0.584	0.223	0.108	0.284	0.952	0.324	0.157	0.47	0.174	0.404	0.664	0.769
	-0.16	0.348	-0.451	-0.308	-0.018	-0.285	0.386	0.202	0.371	0.232	0.123	0.083
Locomotion	0.233	0.988	0.988	0.295	0.28	0.468	0.954	0.379	0.397	0.314	0.523	0.838
	-0.341	-0.004	0.007	-0.301	0.31	0.211	-0.018	0.245	-0.236	-0.279	-0.179	0.058
Presenting	1	**0.01***	0.785	0.109	0.432	0.134	0.361	0.955	0.1	0.404	0.064	0.08
& nursing	-0.002	**-0.661**	0.081	0.447	-0.228	0.42	-0.254	0.016	-0.446	-0.232	-0.49	-0.466
Pup	0.638	0.713	0.904	0.537	**0.043***	0.739	0.602	0.093	0.196	0.067	0.683	0.954
interactions	0.138	-0.108	0.037	0.18	**0.545**	0.098	-0.146	0.449	-0.354	-0.489	-0.115	0.016
Aggression	0.682	0.583	0.716	0.552	0.28	0.336	0.793	0.101	0.763	0.237	0.678	0.233
	0.121	0.161	0.108	0.174	0.31	-0.278	0.075	0.44	-0.086	-0.325	0.117	0.328

8.4.1. Linear models

For both the 2008 and 2009 analyses, the majority of the linear models retained only one covariate, and there was only one instance of collinear covariates being retained within the same model. The following section shall present the results of the linear models for the 2008 and 2009 breeding seasons, separately. For each of the response variables, the eight confidence sets shall be considered collectively and independently.

For the pup daily growth rate, the 'best' model across the 8 confidence sets found that an increase in maternal mass lost per day, coupled with less time spent presenting & nursing, resulted in a heavier pup (Table 8.3; Figure 8.9). This was the 'best' model by $\triangle$ = 12.05, and if the eight confidence sets were considered collectively, then this would be the only model retained. Nevertheless, for the other seven behavioural categories, mothers' daily mass loss was the only covariate retained in the 'best' model (Figure 8.10). However, as the model table suggests (Table 8.3) including presenting & nursing clearly improved the model fit (Figures 8.9 and 8.10). There was also support for maternal postpartum mass (Table 8.3), which also had a positive, influential relationship with pup daily growth rate. The locomotion behavioural category was retained in a model along with duration of lactation, which showed that a longer duration of lactation coupled with less time spent in locomotion, resulted in a heavier pup (Figure 8.11).

For the mass transfer efficiency models, the 'best' model across the 8 confidence sets found that less time spent presenting & nursing resulted in an increase in mass transfer efficiency (Table 8.3 and Figure 8.12). This was the 'best' model by $\triangle$ = 11.7, and if the 8 confidence sets were considered collectively, then this would be the only model retained. As it happens, across the 7 remaining confidence sets, none of the covariates retained within any of the models were influential; therefore, presenting & nursing was the only covariate to influence mass transfer efficiency during the 2008 breeding season.

Tables 8.3 and 8.4: The following two tables show the model output for the 2008 (Table **8.3**) and 2009 (Table **8.4**) analyses. With the exception of the models that retained a behavioural category, the other models comprising the confidence sets were the same (i.e. contained the same reproductive covariates). Therefore, to prevent presenting the same models that were retained within the 8 confidence sets, each of the confidence sets were combined. If a covariate was retained within a model then the estimated effect (Est.) and the standard error of the estimate (SE) are included in the table; '-' indicates that the covariate was not retained within the model; models containing collinear covariates are in bold. The first column of the table (Beh.) states (where relevant) the behavioural category that was retained within the model. The following column notes which of the two response variables (Resp.) are being predicted: pup daily growth rate (PDGR; kg) or mass transfer efficiency (MTE; %). The key for the covariates is as follows: mothers' daily mass loss (MDML; kg), maternal postpartum mass (MPPM; kg), duration of lactation (DURLACT; number of days), behaviour (BEH), date of parturition (DOB). The key for the behaviours is as follows: Resting (R), Comfort Movement (CM), Pup Check (PC), Alert (A), Locomotion (L), Presenting & Nursing (MP), Pup Interactions (PINT), Aggression (AGG).

[1]In Table 8.3, for the PDGR and the MTE analyses, the presenting & nursing (MP) confidence sets retained only one model, both of which contained the MP behavioural category (PDGR $\triangle$ = 12.05; MTE $\triangle$ = 11.7, compared to $\triangle$ = 0*).

[2]In Table 8.3, the resting behavioural category was the 'best' model within its respective confidence set for the MTE analyses ($\triangle$ = 1.832 compared to $\triangle$ = 0*); however, it also retained the other three models that were retained within the other 6 (excluding MP) confidence sets.

Table 8.3

				Covariates										
		Inter.		BEH		MPPM		MDML		DURLACT		DOB		
Beh.	Resp.	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	△
MP[1]	PDGR	0.242	0.298	-7.763	1.781	-	-	0.638	0.084	-	-	-	-	0
		0.437	0.466	-	-	-	-	0.466	0.117	-	-	-	-	0*
L		1.126	0.384	-31.862	11.475	-	-	-	-	0.08	0.022	-	-	3.439
		0.697	0.572	-	-	0.008	0.003	-	-	-	-	-	-	4.815
MP[1]	MTE	0.686	0.026	-1.733	0.391	-	-	-	-	-	-	-	-	0
R^2		-0.067	0.338	0.792	0.416	-	-	-	-	-	-	-	-	0
		0.461	0.09	-	-	-	-	-	-	0.006	0.005	-	-	0*
PC		0.549	0.032	1.694	1.782	-	-	-	-	-	-	-	-	0.854
A		0.526	0.058	0.861	0.955	-	-	-	-	-	-	-	-	0.954
CM		0.603	0.032	-1.779	2.022	-	-	-	-	-	-	-	-	0.995
AGG		0.599	0.031	-4.039	5.533	-	-	-	-	-	-	-	-	1.261
PINT		0.58	0.03	-0.159	1.45	-	-	-	-	-	-	-	-	1.856
L		0.576	0.028	0.069	2.704	-	-	-	-	-	-	-	-	1.869
		0.472	0.119	-	-	<0.001	<0.001	-	-	-	-	-	-	2.826
		0.675	0.116	-	-	-	-	-0.025	0.029	-	-	-	-	2.878
		0.648	0.126	-	-	-	-	-	-	-	-	-0.002	0.003	3.329

Table 8.4

				Covariates										
		Inter.		BEH		MPPM		MDML		DURLACT		DOB		
Beh.	Resp.	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	△
	PDGR	1.057	0.409	-	-	-	-	0.301	0.108	-	-	-	-	0
		1.908	**0.502**	**-**	**-**	**0.005**	**0.002**	**-**	**-**	**-**	**-**	**-0.018**	**0.009**	**1.881**
		1.266	0.439	-	-	0.005	0.002	-	-	-	-	-	-	2.596
		2.836	0.361	-	-	-	-	-	-	-	-	-0.018	0.01	3.759
		1.379	0.551	-	-	-	-	-	-	0.042	0.028	-	-	4.722
CM		2.011	0.143	9.313	6.654	-	-	-	-	-	-	-	-	4.979
A		1.94	0.202	4.078	3.088	-	-			-	-	-	-	5.196
	MTE	0.886	0.105	-	-	-	-	-0.08	0.028	-	-	-	-	0
AGG		0.551	0.027	7.459	5.131	-	-	-	-	-	-	-	-	1.137
PINT		0.492	0.039	4.758	1.869	-	-	-	-	-	-	-	-	1.353
CM		0.54	0.037	2.284	1.74	-	-	-	-	-	-	-	-	5.552
R		1.022	0.348	-0.543	0.432	-	-	-	-	-	-	-	-	5.699

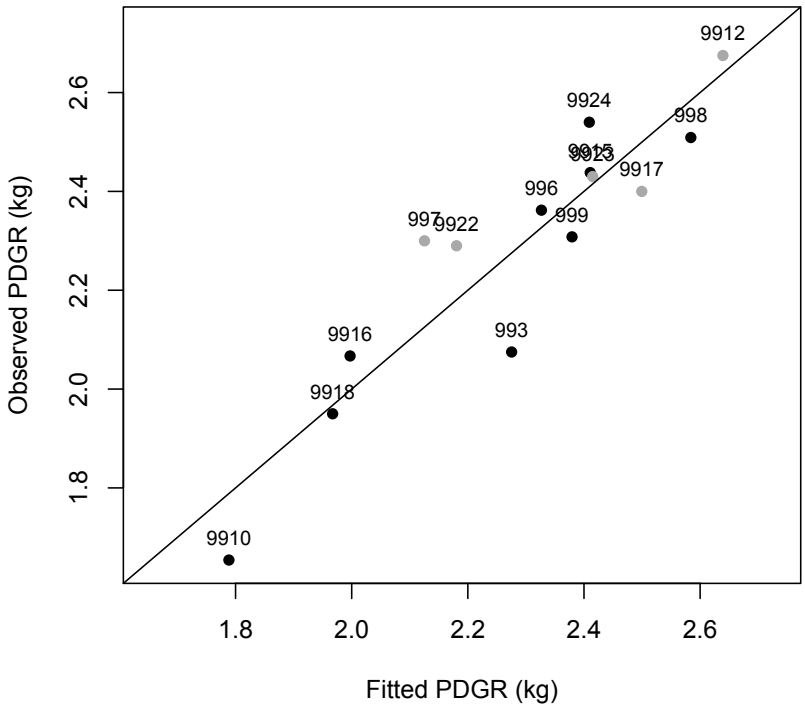


Figure 8.9: The fitted and observed values for the pup daily growth rate (kg) for the model containing the presenting & nursing behavioural category and the mother's daily mass loss (kg) for the females seen in the 2008 breeding season. The age (in years) of these females are shown in the legend for Figure 8.1.

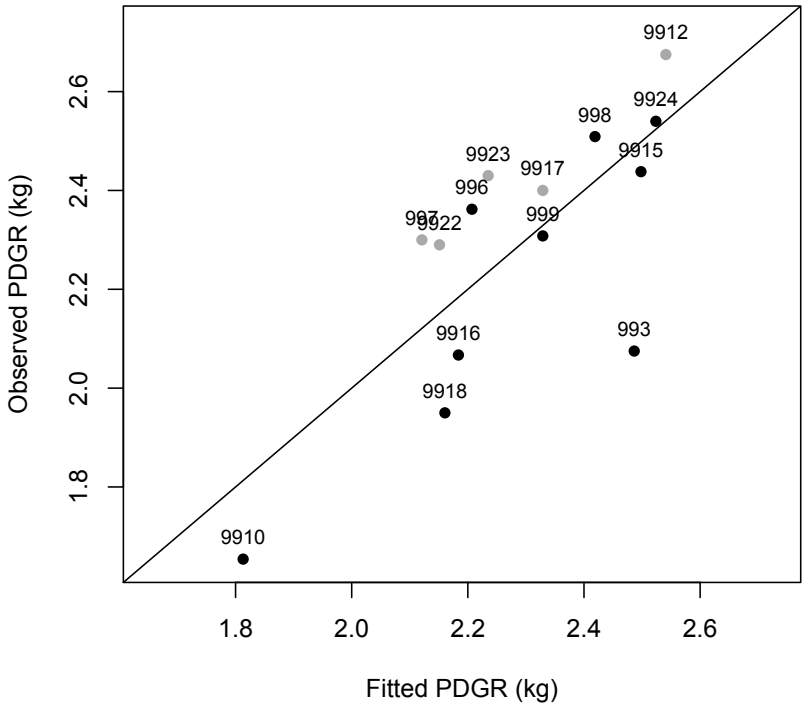


Figure 8.10: The fitted and observed values for the pup daily growth rate (kg) for the model containing mother's daily mass loss (kg) for the females seen in the 2008 breeding season. The age (in years) of these females are shown in the legend for Figure 8.1.

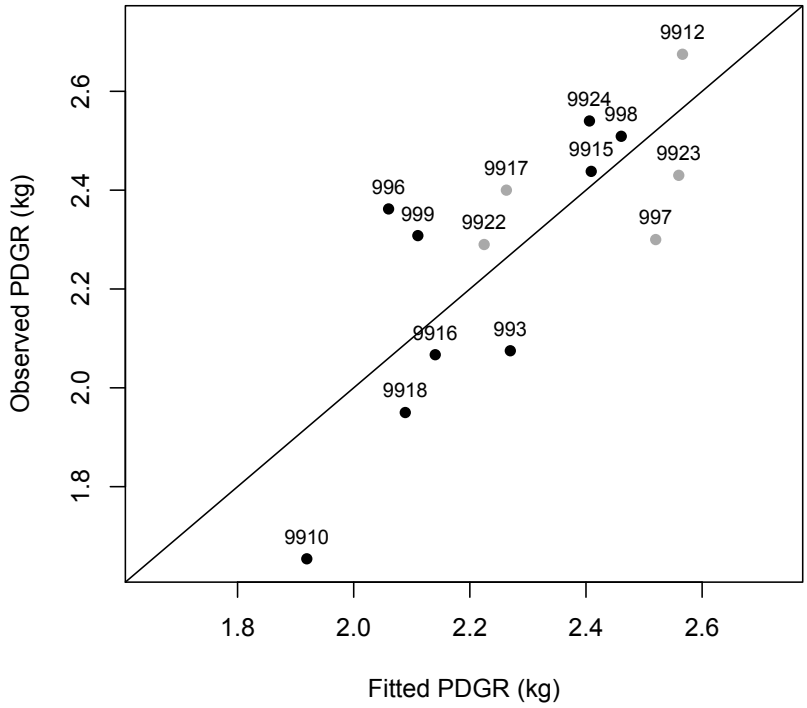


Figure 8.11: The fitted and observed values for the pup daily growth rate (kg) for the model containing the locomotion behavioural category and the duration of lactation (days) for the females seen in the 2008 breeding season. The age (in years) of these females are shown in the legend for Figure 8.1.

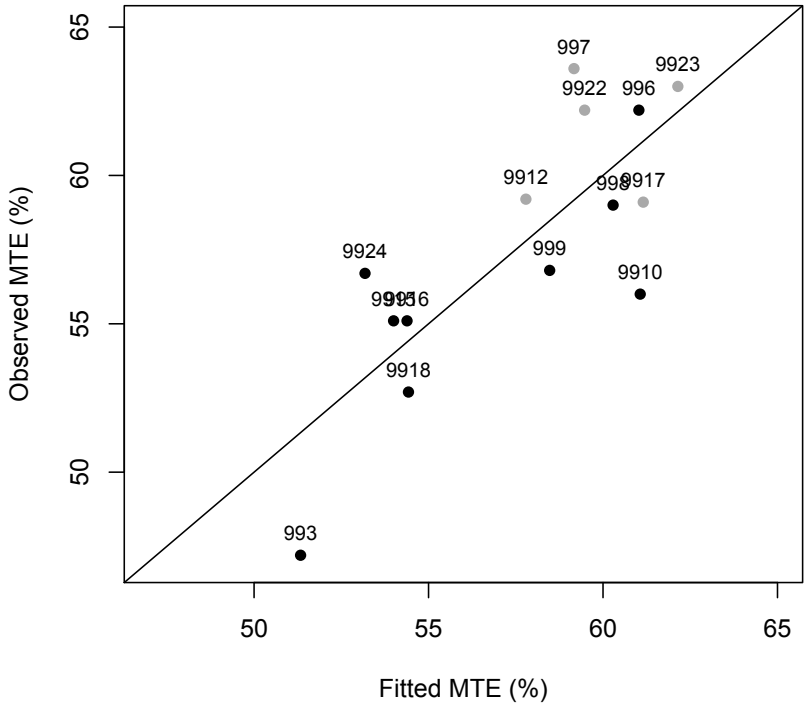


Figure 8.12: The fitted and observed values for the mother-pup mass transfer efficiency (%) for the model containing the presenting & nursing behavioural category for the females seen in the 2008 breeding season. The age (in years) of these females are shown in the legend for Figure 8.1.

For the pup daily growth rate, the 'best' model across the 8 confidence sets found that an increase in the maternal mass lost per day resulted in an increase in pup mass gain per day (Table 8.4 and Figure 8.13). There was also support for heavier mothers producing heavier pups. However, none of the other 4 covariates (duration of lactation, date of parturition, comfort movement and alert) retained across the 8 confidence sets were influential. Conversely, for the mass transfer efficiency, the 'best' model across the 8 confidence sets found that a decrease in the maternal mass lost per day, resulted in an increase in mother-pup mass transfer efficiency (Table 8.4); however, the model did not fit these data well (Figure 8.14). No other reproductive covariate was retained in any of the 8 confidence sets. Of the behavioural covariates, the resting, comfort movement, aggression and pup interactions behaviours were all retained within their respective confidence sets; however, only the latter was influential. Nevertheless, the model did fit the pup interactions data well (Figure 8.15).

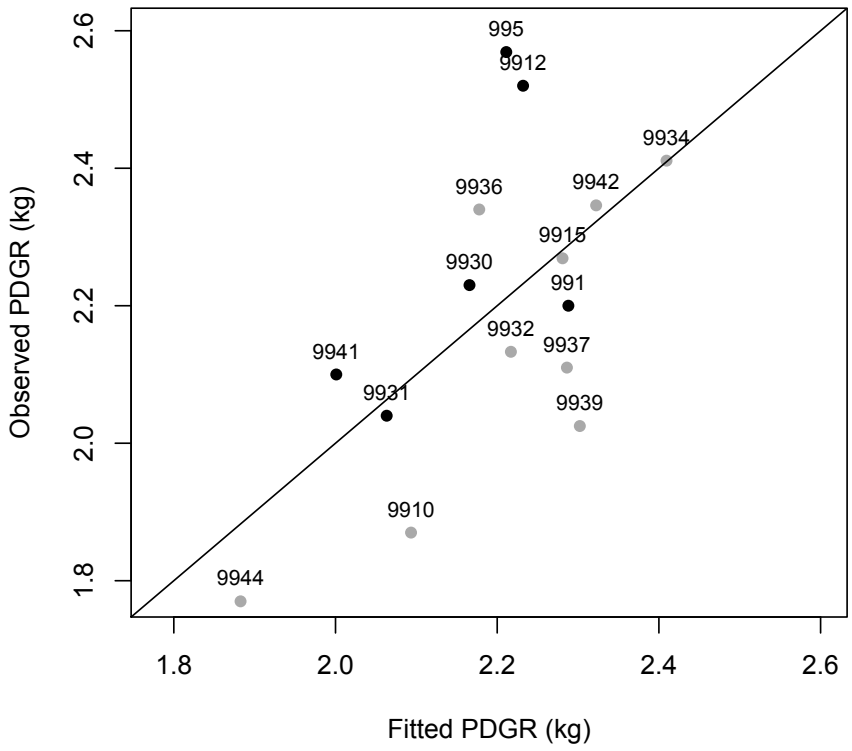


Figure 8.13: The fitted and observed values for the pup daily growth rate (kg) for the model containing the mother's daily mass loss (kg) for the females seen in the 2009 breeding season. The age (in years) of these females are shown in the legend for Figure 8.1.

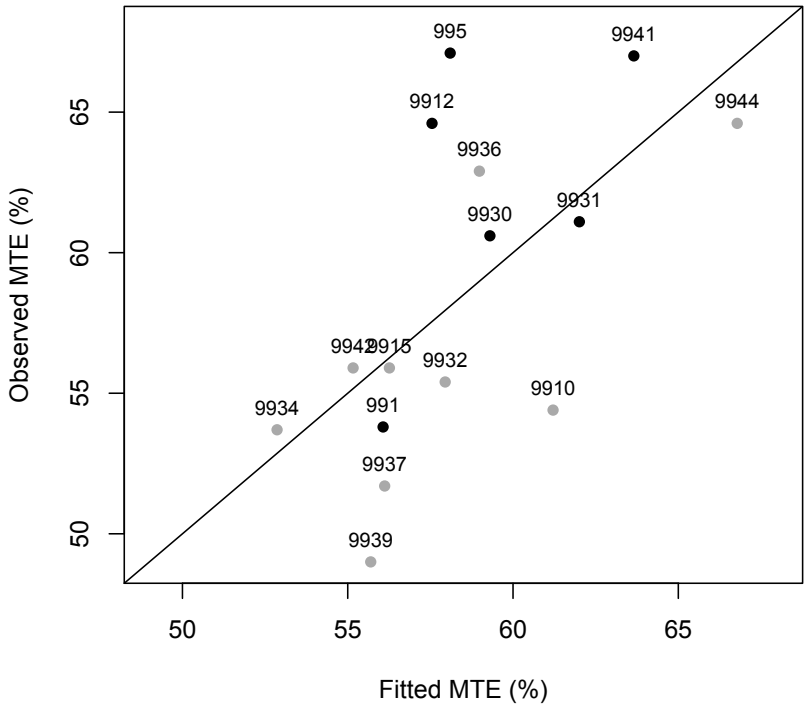


Figure 8.14: The fitted and observed values for the mass transfer efficiency (%) for the model containing the mother's daily mass loss (kg) for the females seen in the 2009 breeding season. The age (in years) of these females are shown in the legend for Figure 8.1.

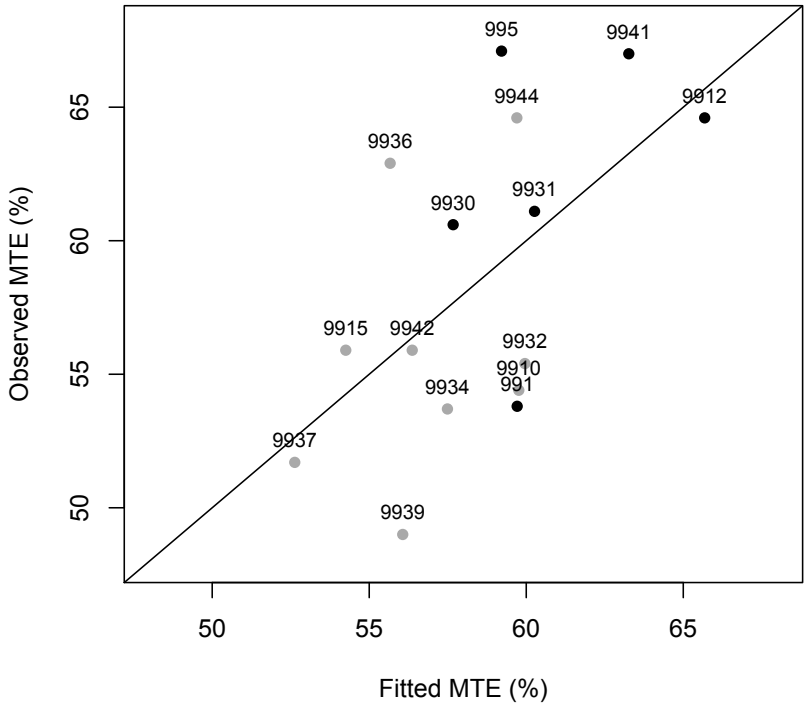


Figure 8.15: The fitted and observed values for the mass transfer efficiency (%) for the model containing the pup interactions behavioural category for the females seen in the 2009 breeding season. The age (in years) of these females are shown in the legend for Figure 8.1.

8.5. Discussion

Despite the influence of the reproductive covariates, there was some evidence that individual variation in behaviour did influence pup daily growth rate and mass transfer efficiency. As far as Ross Culloch (RMC) is aware, this is the first study to include individuals' behaviour (whilst on the breeding colony) as a covariate in a model predicting the variance in these commonly used short-term proxies for fitness. The findings presented in this chapter are discussed below with reference to previous studies on grey seals, and more broadly, other species of pinniped. The potential influence of covariates that were not included in the model shall be discussed, prior to considering the potential influence of CIDs in behaviour on pup daily growth rate and mass transfer efficiency.

8.5.1. Explaining the variation in pup growth rate and mass transfer efficiency

For both breeding seasons, there were two competing models for the pup daily growth rate. These models showed that heavier females produced heavier pups; and females that lost more mass per day, produced heavier pups. As shown in previous studies on grey seals (e.g. Iverson et al., 1993; Pomeroy et al., 1999), both of these reproductive covariates (MDML and MPPM) were collinear with one another. Consequently, many studies, spanning a broad range of pinniped species, have used ne or the other of these covariates to show that there is a strong correlation between maternal mass and the mass of the pup at weaning (e.g. grey seals, Anderson & Fedak, 1987; Iverson et al., 1993; Pomeroy et al., 1999; Weddell seals (*Leptonychotes weddellii*), Wheatley et al. 2006; Southern elephant seals (*Mirounga leonina*), Arnbom et al., 1997; harbour seals (*Phoca vitulina*), Bowen et al., 2001; see also reviews by: Kovacs & Lavigne, 1986b; Boness & Bowen, 1996; Trillmich, 1996).

For the 2009 breeding season, the maternal postpartum mass and mothers' daily mass loss were the only influential covariates retained in the models for the pups' daily growth rate. However, for the 2008 breeding season, there was support for the locomotion and the presenting & nursing behavioural categories. The first

of these models showed that less time spent in locomotion coupled with a longer duration of lactation resulted in a heavier pup, which suggests that energy used in locomotion could have been invested in the pup (by staying longer on the colony). This may have been driven more by the environment, given that the analyses of the SA and the north study area (NSA) data showed that locomotion was not repeatable, and was better predicted by extrinsic covariates (Chapter 4, Table 4.2; Chapter 5, Section 5.4.5). Given that the rainfall and air temperature for 2008 were considered to be 'typical' (higher temperatures at the beginning, and higher rainfall at the end of the breeding season) as compared to the 'atypical' conditions in 2009 (lower temperature and higher rainfall at the beginning of the breeding season; Chapter 3, Section 3.14) then the influence of locomotion might be an indication of the potential costs attributed to mothers that commute greater distances between pools of water and their pup (Twiss et al., 2000; Redman et al., 2001; Twiss et al., 2002; Chapter 3, Section 3.14). In other words, in 2009, the trade-off between pool and pup may have been considerably reduced (due to the cooler temperatures and greater availability of pools) and, as a consequence, mothers were able to remain close to a pool of water and their pup. Conversely, the 'typical' weather conditions in 2008 may have augmented the pup-pool trade-off, which would have been reflected in the proportion of time an individual spent in the locomotion behavioural category.

The model retaining presenting & nursing was the 'best' model across all 8 of the confidence sets. This model showed that less time spent presenting & nursing, coupled with a greater daily mass loss, resulted in a heavier pup. Furthermore, for the mass transfer efficiency models in the 2008 breeding season, the presenting & nursing behaviour was also retained in the 'best' model across the eight confidence sets. In this instance, the model showed that less time spent presenting & nursing resulted in an increase in the mass transfer efficiency. Although these results may appear counterintuitive, females are often observed to relocate during presenting & nursing bouts, such that the event is rather stop-start (and it is not clear why females do this; Culloch, pers. obs). Perhaps this behaviour is influenced by proximity to conspecifics (Pomeroy et al., 1994; Caudron, 1998; Stephenson et al., 2007) or unsuitable/awkward terrain (e.g. too rocky; Twiss et al., 2000; Twiss et al., 2001); consequently, the female relocates

further from conspecifics and/or to an area where the terrain is more suitable. Conversely, other mothers simply present and the pup suckles almost immediately (Culloch, pers. obs.). Therefore, if individuals consistently behaved this way within a breeding season (rather than it being a product of younger, less experienced pups taking longer to suckle, for example), then this relationship could be explained by a combination of the social and physical environment and/or the mothers' behaviour. However, there are other factors, such as mothers' age and pup sex, which may also influence this relationship; these shall be discussed in greater detail, in Sections 8.5.2 and 8.5.3, respectively.

For the mass transfer efficiency models for the 2009 breeding season, the mothers' daily mass loss and pup interactions were retained in two separate models. The model for the former did not fit these data well; conversely, the model for the latter did fit these data well. For this model, more time spent interacting with the pup, resulted in an increase in mass transfer efficiency. This may be related to the mother-pup bond, such that more time spent interacting with the pup improves this bond, which results in a more efficient mass transfer. Therefore, with the exception of presenting & nursing in 2008 and pup interactions in 2009, there is very limited evidence that the mass transfer efficiency was influenced by any of the covariates included in the global models for either breeding season. This lack of a relationship between mass transfer efficiency and mothers' postpartum mass has also been shown in ice-breeding grey seals in Canada (Lydersen et al., 1994; Lydersen et al., 1995). However, this population is known to feed at sea during lactation, which would influence the relationship between these two variables (Lydersen et al., 1995; Baker et al., 2005). Conversely, seals on North Rona do not return to the sea to feed during lactation, yet studies on this breeding colony have also shown that there is no relationship between mass transfer efficiency and the mothers' mass at parturition (Pomeroy et al., 1999). Therefore, irrespective of whether individuals feed during lactation or not, there does not appear to be a correlation between measures of maternal mass and mass transfer efficiency in grey seals.

8.5.2. The age and experience of the mother

Despite the relatively small number of known-age individuals included in the present study, a qualitative assessment suggests that the age of the mother did not influence the relationship between any of the reproductive and/or behavioural variables. Pomeroy et al. (1999) did include mothers' age in their analyses, which showed that age did not play a significant role in the success or failure of a mother raising her pup (where 'failure' was defined as the female failing to give birth, the pup dying, or the pup failing to reach a threshold mass of 30 kg pre-weaning). The ages of the mothers included in Pomeroy et al.'s (1999) study ranged from 4 to 36 years old; therefore, their analyses included both younger and older mothers, which suggests that age (as a proxy of maternal experience) is not influencing the mass of the pup at weaning. These findings are supported by recent studies on Sable Island, Canada, where Lang et al. (2011a, b) compared the maternal energy expenditures, and pup growth and energy deposition of primiparous and multiparous individuals over the duration of lactation. They concluded that primiparous females weaned pups of the same relative size and condition as multiparous females without expending proportionally more energy.

Lang et al. (2011a, b) also found that primiparous mothers had a higher number of nursing bouts per hour, which did result in a significantly greater proportion of time spent nursing compared to multiparous mothers (Lang et al., 2011a). Although there was no significant difference in milk composition (and thus energy content) between these two groups of females, primiparous females had a significantly lower daily milk energy output than multiparous females, which they suggested was a result of a reduced physiological capacity for milk secretion (which has been shown in other species, see references therein; Lang et al., 2011a, b). Furthermore, they also found that primiparous females were significantly more active than multiparous females (although the difference between the groups was less than 4% of the overall time budget, on average). Therefore, although age does not appear to influence pup mass at weaning, it may influence how an individual partitions their activity budget. Consequently, these findings suggest that, where sample sizes allow, an interaction term between behaviour and age should be included in the models.

8.5.3. Pup sex and differential investment

There are a large number of studies, covering a broad range of pinniped species, which have found evidence for and against differential investment (**For:** e.g. grey seals, Kovacs & Lavigne, 1986a; Anderson & Fedak, 1987; Baker et al., 1995; Galapagos fur seals (*Arctocephalus galapagoensis*), Trillmich, 1986; Antarctic fur seals (*A. gazella*), Goldsworthy, 1995; Juan Fernandez fur seals (*A. philippii*), Osman et al., 2010. **Against:** e.g. grey seals, Bowen et al. 1992; Smiseth & Lorentsen, 1995b; Pomeroy et al., 1999; Northern elephant seal (*M. angustirostris*), Kretzmann et al., 1993; Southern elephant seal, Campagna et al., 1992; Antarctic fur seal, Lunn & Arnould, 1997; harbour seal, Bowen et al., 1992). In the present study, because the pup sex data were skewed within breeding seasons, it was not possible to quantitatively address this. However, qualitatively, there was no evidence to suggest that pup sex influenced the relationship between the reproductive and/or behavioural variables. With respect to grey seals, based on the data available at the time, Trillmich (1996) suggested that there was little evidence to support differential investment in this species. Since then, Pomeroy et al. (1999), using 16 years of data from North Rona, have added considerable weight to the argument that mothers do not invest more (or less) in male offspring.

8.5.4. The influence of individual variation

The influence of individual variation in behaviour has been addressed throughout this thesis (Chapters 4 - 7); therefore, it shall not be discussed here. However, other studies have investigated individual variation in other phenotypic traits. Most relevant to this study, Lang et al. (2009) addressed the repeatability of lactation performance of female grey seals on Sable Island, Canada. They found that milk composition (protein; $r = 0.38$ fat; $r = 0.5$), daily milk output ($r = 0.46$) and the duration of lactation ($r = 0.57$) where all repeatable. Consequently, if these CIDs in lactation performance also occur among the females on North Rona, then this could explain the inter-annual differences in the relationships of some of the covariates, such as mother's daily mass loss and mass transfer efficiency (which had a negative relationship in both breeding seasons, but was only significant in 2009).

8.5.5. The measure of success

In the present study all females were, by definition, successful mothers because they raised their pup to weaning. If a female does not pup (i.e. is not pregnant) or if her pup dies, then that female will typically remain on the colony (or at least, within a region of the colony) for a relatively short period of time (Culloch, pers. obs.). In these scenarios, it is difficult to quantify behaviour (because the situation and/or context is different) and fitness (because there is no fitness measure, other than the pup is dead as opposed to alive). Therefore, the results presented here are based on a range of successful females, some of which were more successful than others. Furthermore, female grey seals are known to breed from 4 through to 42 years of age (Pomeroy et al., 1999; Bowen et al., 2006); therefore, data from two breeding seasons should be regarded as a brief insight into a mothers' reproductive success (raising a pup to weaning), which may not be representative of their reproductive output across their lifetime. Nevertheless, the findings presented here compliment those of Pomeroy et al. (1999), which suggests that heavier mothers produce heavier pups, and that individual variation is likely to influence pup weaning mass (and perhaps mass transfer efficiency). However, teasing apart the influence of individual variation in behaviour from other influential covariates, such as environmental variation (e.g. rainfall and air temperature; Twiss et al., 2002; Chapter 3, Section 3.14), and social associations (Pomeroy et al., 2005), would require a substantially larger dataset, both with respect to individuals and breeding seasons.

8.5.6. Consistent individual differences (CIDs) in behaviour

Chapters 4, 5, 6 and 7 of this thesis have shown that certain aspects of the behaviour of wild postpartum female grey seals are repeatable. Of the three behavioural categories that were influential in the analyses presented in this chapter, presenting & nursing was not repeatable in the SA, and although robustly repeatable in the NSA (repeatable in 3 out 4 of the analyses) it had the lowest (significant) repeatability estimates of the 5 repeatable behaviours. There was a similar pattern for the pup interactions behavioural category, and locomotion was not repeatable in any of the four analyses for either study site (Chapter 4, Table

4.2 and Chapter 7, Table 7.1). Therefore, there was no evidence that the more robustly repeatable behaviours (and in particular, alert) had any influence on the pup daily growth rate or the mass transfer efficiency. This shall be discussed in more detail in Chapter 9.

8.6. Conclusion

As far as RMC is aware, this is the first study to consider how the mechanistic mass transfer relationship between mother and pup might be affected by individual differences in behaviour. However, the reproductive variables considered in parallel with the behavioural measures in this chapter offer a limited preliminary assessment of how a mother's behaviour during lactation may affect her and her offspring. Consequently, future research should apply this analytical approach to a larger subset of the long-term, longitudinal dataset from North Rona, which would undoubtedly provide an important insight into the ecological and evolutionary importance of (consistent) individual differences in the behaviour of wild animals.

Chapter nine:
General discussion

9.1. Introduction

Using a purely 'hands-off' observational approach, this thesis has shown that certain aspects of the behaviour of wild postpartum female grey seals were repeatable. In order to do this, a novel three-step analytical approach was developed, where the results of each step supported the results of the subsequent step(s). This progressive approach was deemed necessary, because the underlying assumptions of the analytical techniques used could not always be fully met. For the north study area (NSA) data, the first step of the analyses showed that not all behaviours were robustly repeatable (Chapter 4). Based on previous studies (Twiss & Franklin, 2010; Twiss et al., 2011a) and the results for each step of the analyses presented in this thesis (Chapters 4, 5 and 6), only the pup check and the alert behavioural categories were analysed in all three steps. For both of these behaviours, the pattern in the results was consistent throughout; pup check was highly repeatable, but was not robust, whereas alert was both highly repeatable and robustly repeatable (Chapter 4, 5 and 6). Focusing on these two behavioural categories, the three-step analytical approach was applied to an independent dataset collected in the study area (SA). The results of these analyses found similar patterns in the SA datasets for both behaviours (Chapter 7), but they were less apparent than the patterns in the NSA datasets. These findings do raise important questions regarding the function of pup checking and alert, and the mechanism(s) that might influence individual variation in these behaviours. Prior to addressing these questions, the important methodological considerations that were raised during the comparisons within (Chapter 2) and between (Chapter 7) the two study sites shall be addressed first.

9.2. Methodological considerations

9.2.1. The suitability of the scan sampling protocol

The comparison between the focal and scan sampling approaches showed that at the population-level, there was no significant difference between the focal and scan sampling approaches for the pup check or the alert behavioural categories. Although pup check was not a frequently recorded behaviour, it did comprise two to three times more of the activity budget than locomotion and aggression (both of which were also included in step 2 of the analyses for the NSA data). Consequently, scan sampling was considered to be a suitable sampling approach for both the pup check and the alert behavioural categories. Conversely, the proportion of time spent in the comfort movement and pup interactions behavioural categories was significantly greater when the scan sampling approach was used (Chapter 2, Section 2.5.4). Consequently, scan sampling at five minute intervals is unlikely to give an accurate representation of all eight of the behavioural categories. Furthermore, even if a significant difference between the two approaches did not occur, it does not necessarily mean that either approach is suitable. For behaviours that occur infrequently and for short (e.g. locomotion and aggression) or long (e.g. presenting & nursing) durations a more intensive 'all-occurrence' approach may be better suited in order to obtain a representative sample of these behaviours (Altmann, 1974; Martin & Bateson, 2002).

9.2.2. Sample sizes: individuals, scan samples and spatial samples

For the alert behaviour (and particularly in the NSA), repeatability remained robust, despite a relatively small number of individuals. However, for the pup check behaviour, the significant repeatability estimates for both study sites were obtained from the groups that had the highest number of re-sighted individuals. Given that the median percentage of time spent in the pup check behaviour (median = 1.97, IQR = 1.29; Chapter 3, Table 3.1) was considerably lower than the alert behaviour (median = 6.04, IQR = 2.63; Chapter 3, Table 3.1), it may be that the percentage of time individuals spend pup checking is similar, as there is generally less (absolute) spread in the between-individual variation. Therefore, to

identify CIDs in behaviours that are recorded infrequently (and therefore account for a small proportion of the activity budget), it is essential that the spread of between-individual variation in the population is captured. Consequently, the best approach for doing this would be to increase the sample size of individuals.

In step 2 of the analyses for the NSA, the locomotion and the aggression behavioural categories were modelled. However, it was not possible to model the 2007 datasets because there were too few occurrences of these behaviours. This was a result of the smaller numbers of scan samples collected during this breeding season, coupled with the rarity of these behaviours (Chapter 2, Section 2.5.4 and Chapter 3, Table 3.1). Conversely, the 2007 datasets for the pup check and alert behavioural categories were modelled in step 2. However, the patterns in these data were not as apparent as they were for the corresponding 2008 and 2009 datasets. Furthermore, the patterns seen in the results for the 2007 datasets were very similar to those seen in the results of the SA analyses for these two behaviours, for all three breeding seasons. Therefore, the comparatively smaller number of scan samples collected in the SA and in the NSA in 2007, appear to have had a considerable influence on the ability of the models to fit the observed data. Consequently, these comparisons suggest that a minimum number of scan samples (which is greater than 3 hours per day, based on the NSA data collected in 2007), is required in order for the models to adequately fit these data.

Spatial data were collected in the NSA at hourly intervals (Chapter 2, Section 2.5.5). As the NSA covers a relatively small area, and because behavioural observations typically occurred over the entire day, known individuals were almost always identified on the hourly maps. Consequently, the average number of locations per known individual was approximately 100. Conversely, spatial data were collected in the SA at daily intervals (Chapter 7, Section 7.3.1). The mother-pup distances were not available for the SA, and the number of locations per individual did not exceed 16, which was too few samples to accurately calculate the home range (kernel density estimate, KDE). Furthermore, with such small sample sizes, the spatial data for the SA may not provide an accurate representation of the social and environmental variation that an individual

experiences whilst on the breeding colony. These issues are revisited in Section 9.2.4, below.

9.2.3. Individual variation in behaviour during lactation

For both the NSA and SA datasets, only individuals with ≥ 200 scan samples were included in step 1 of the analyses (Chapter 3, Section 3.4, Chapter 4 and Chapter 7). By applying this cut-off to both study sites, it was expected that the estimates of repeatability for the respective behaviours would be similar. However, there was considerable variation in the ICCs between the two sites (which was particularly true for the behavioural categories that were not considered further; Chapter 4, Table 4.2 and Chapter 7, Table 7.1). This variation could, in part, be explained by the individuals included in the samples (Section 9.2.2) or the variation in the social and/or environmental conditions between the two study sites (Section 9.2.4). However, another potentially contributing factor could be that the beginning of lactation, which was rarely sampled in the SA (Chapter 7, Appendix, Tables A7.1 - A7.3) is important for identifying repeatability in certain behaviours. This supposition is supported by the exploratory analyses of the NSA data (Chapter 3, Section 3.6 and Chapter 4, Appendix, Table A4.1), which did show that the proportion of time spent in some of the behaviours varied significantly across the lactation periods. Furthermore, the home range usage (which was not calculated for the SA) also varied significantly across the lactation periods, with females moving closer to the core area of their home range during mid and late lactation. Conversely, during early lactation, females were further from the core area of their home range, and there was considerably more variation in females' location within their home range. Therefore, these findings lend further support to the potential importance of individual variation in behaviour during the first few days postpartum.

9.2.4. Potentially influential covariates and the temporal resolution of data collection

For the NSA data, all covariates that were thought to (or were known to) influence behaviour were included in the models. Furthermore, with the exception

of rainfall, all continuous covariates were collected at the same temporal resolution as the response variable. Conversely, for the SA data, only the activity of the pup and air temperature were collected at the same temporal resolution as the response variable. Consequently, this coupled with small sample sizes for the spatial data (Section 9.2.2), may explain, in part, why the patterns in the results for steps 2 and 3 were not as pronounced in the SA data as they were for the NSA data. This variation in the temporal resolution of data collection may also explain why the alert behaviour was not robustly repeatable in step 3 of the analyses for the SA data. As noted in Chapter 6, Section 6.2, the BLUP represents the variation for individual *x*, which has not been captured by the covariates included in the model. Therefore, by omitting (or inadequately accounting for) influential covariates, the BLUPs capture the additional unexplained variation, which would ultimately influence the repeatability estimate. Consequently, these comparisons suggest that it is fundamentally important to include covariates at an appropriate temporal scale, and that all potentially influential covariates should be included in the models.

For the NSA data, the models for the aggression behavioural category in step 2 of the analyses failed to fit the observed data for the 2008 and 2009 breeding seasons. This suggests that additional covariates, such as information on social associations (Pomeroy et al., 2005; Ruddell et al., 2007), may be required in order to explain the variance in this behaviour. For other infrequently occurring behaviours, such as locomotion (for which the models fit the observed data relatively well) and presenting & nursing, the response variable could be more informative. For example, the proportion of time spent away from the pup may be a more biologically relevant measure of locomotion, especially given that this behaviour is (perhaps almost entirely) driven by the pup-pool trade-off (Redman et al., 2001; Twiss et al., 2002). The total time spent presenting & nursing or the number of bouts per hour may be a more biologically relevant measure for this behavioural category. Furthermore, who initiated and who ended each bout may also be an important covariate to include in the presenting & nursing models (Smiseth & Lorentsen, 2001). Not all of these data are available for the present study (primarily due to trade-offs between sampling techniques); however, for future studies, and for researches that wish to focus on a particular behaviour, it is

important to consider which additional variables may be required to better explain the variance in the behavioural categories of interest.

The exploratory analyses for the SA suggested that pools were more abundant and/or widely distributed in the SA than they were in the NSA. As the pool coverage for the SA was from the 1994 breeding season, it might not have been fully representative of the distribution of pools in 2008, 2009 and 2010. Nevertheless, assuming that there was no gross change in the distribution of pools between these breeding seasons (Twiss, pers. obs.), the data suggest that being closer to pools of water reduces the influence of the weather parameters (Twiss et al., 2000; Redman et al., 2001; Twiss et al., 2002), which, based on the collinearity analyses, also reduces the density and the distance to the nearest female neighbour (Chapter 7, Appendix, Tables A7.10 - A7.18). The closer proximity of seals to pools in the SA may be facilitated by the gradual decline in the number of breeding seals in the SA over the last decade (the decline is likely to have occurred throughout the North Rona breeding colony, see Chapter 2, Section 2.3). Consequently, by being closer to pools of water, females in the SA are able to reduce the influence of the pup-pool trade-off (Redman et al., 2001; Chapter 7, Section 7.5.5.4), which may, in turn, reduce the likelihood of permanent mother-pup separation (which can lead to pup mortality; Anderson et al., 1979; Baker, 1988). The topographic variation between the NSA and the SA (with respect to the distribution and abundance of pools) may account for some of the behavioural differences between the two study sites (Chapter 7, Section 7.3.5). Consequently, the manner in which individuals utilise their local environment in the SA may be considerably different to the NSA. To ascertain whether or not this is the case, the same spatial data collected at the same temporal resolution for the NSA would be required for the SA. Given that the SA covered too great an area to map at an hourly interval, the best approach here would be to map only the target individuals at this temporal resolution.

The comparison between the activity budgets for the SA and the NSA highlighted some of the trade-offs associated with each of the study sites (Chapter 7, Section 7.3.5). Specifically, the SA had a better vantage point covering a larger area, but target individuals were further from the observer. Consequently, the

observer in the SA may not have been in the best location for recording subtle behaviours (such as comfort movements). However, in the SA, with a better vantage point, it was possible to gather data on more individuals, over a comparably larger range of terrain (Twiss et al., 2000). Furthermore, a better vantage point may reduce the proportion of time individuals are recorded as out-of-sight (see below), and it may also increase the likelihood of being able to observe whether or not a mother is presenting or nursing. Conversely, the observer in the NSA was considerably closer to target individuals at ground level, which allowed the observer to gather data on subtle behaviours and (given the smaller area) made it possible to map the individuals at hourly intervals. However, at ground level, even shallow gullies can result in individuals being out-of-sight for a greater percentage of time, as was shown in the comparison of the gross activity budgets (NSA: median = 0.06, IQR = 2.02, Chapter 3, Table 3.1; SA: median = 0.00, IQR = 0.018, Chapter 7, Appendix, Table A7.4). Therefore, the location of the observer in relation to target individuals is an important consideration with respect to the resolution to which certain data can be collected.

9.2.5. Developing guidelines for quantifying CIDs in the behaviour of wild animals

To ascertain which of these differences in the sampling protocol affected the outcome of the results, the best practice would be to systematically alter the NSA dataset to mirror the limitations of the SA dataset. In other words, model the NSA data using one map per day, omit potentially influential covariates, use only the mid and late lactation periods and use a pool coverage from a different breeding season to extract the distance to nearest pool data. Therefore, by applying each of these limitations to the NSA data, one at a time, it would be possible to identify which (if any) element of the SA sampling protocol causes the greatest deviation from the repeatability estimates obtained using the complete NSA dataset.

These simulations would be a time consuming process and were out-with the time constraints of the thesis; however, they shall be undertaken at a later date. Nevertheless, it is predicted that if all of these limitations were placed on the

NSA data then the repeatability estimates for the eight behaviour categories would vary considerably from those attained using the complete dataset. Prior to carrying out these analyses, in order to successfully identify CIDs in behaviour (where they exist), it is suggested that behavioural observations are undertaken regularly (> 3 hours per day; rather than intermittently) throughout lactation, and that, as many individuals as possible are included in the observations. For the spatial data, maps should be collected regularly, and an absolute minimum of ca. 2 - 3 locations per individual, per day would be required in order to accurately calculate the home range (KDE) (Chapter 7, Section 7.3.2). However, this sampling protocol will depend on the behaviour of interest and the study species.

9.3. CIDs in behaviour: the ecological and evolutionary perspective

Pup check and alert were the only behaviours analysed in all three steps for both the NSA and the SA; therefore, only these two behaviours shall be considered in this and the subsequent sections. Comparisons between the observational data presented here and the 'classic' behavioural axes (Réale et al., 2007; Chapter 1, Section 1.3) were made, briefly in Chapter 4, Section 4.7.4. Of the five behavioural axes, the definition of 'shyness-boldness' was considered to be the most suitable for the pup check and the alert behavioural categories. However, in the present study, these behaviours were deliberately kept separate based on their functionality (see below). Moreover, to identify whether or not (and to what extent) CIDs in behaviour influence wild populations, it is fundamentally important that functionally different behaviours are not considered as synonymous. Consequently, for observational studies of wild animals, it may be more pragmatic to concentrate on the 'natural' behaviour, rather than attempting to coarsely define behaviours on experimental axes that may, or may not have any ecological relevance to the questions posed.

For both the NSA and the SA, the pup check behaviour was not robustly repeatable. As discussed in the preceding sections, this may have been influenced by a number of factors. Furthermore, as was briefly discussed in Chapter 7, Section 7.5.4 the influence of the pup across breeding seasons (because it is a different individual) is likely to be an important covariate. In other words, if pups

show (consistent) individual differences in their behaviour (as the adult females and adult males have been shown to do; Twiss & Franklin, 2010; Twiss et al., 2011a; Chapters 4, 5, 6, and 7), then this would presumably influence a mother's behaviour across breeding seasons. Another potentially influential factor could be the health and/or condition of the pup within breeding seasons, which is also likely to affect the pups' behaviour, and in turn, influence the mothers' behaviour.

In the present study, the lactation period analyses found that mothers spent significantly more time pup checking during the earlier stages of lactation (Chapter 3, Section 3.6). This was expected, given that pup mortality (resulting from the mother-pup bond not forming or being broken), is more likely to occur shortly after birth (Anderson et al., 1979; Baker, 1988). However, for steps 2 and 3 of the NSA analyses this covariate was omitted from the analyses because it was consistently collinear with home range and rainfall (and for certain datasets, it was also collinear with several of the other covariates too). Therefore, for the NSA analyses, it is not possible to say with confidence that the pup check behaviour was not influenced by the age of the pup. With respect to the SA, pup age was included in the models and was infrequently retained in some of the best models for steps 2 and 3 of the analyses (Chapter 7, Section 7.4). However, the models did not fit the observed data well, which was thought to be the result of omitting influential covariates from the analyses of the SA data (see Section 9.2.4). Nevertheless, in steps 2 and 3 of the analyses for both study sites, the models showed that the more active the pup was, the more time the mother spent pup checking (Chapters 5 and 6). Therefore, there is evidence to suggest that the pup check behaviour may not be dictated entirely by the mother (Fogdon, 1971; Kovacs, 1987; Smiseth & Lorensten, 1995a, b; Smiseth & Lorensten, 2001), and as a result, this may offer an alternative explanation as to why pup checking is not robustly repeatable.

The alert behaviour was robustly repeatable and remained robust even after accounting for the influence of other covariates (Chapters 4, 5 and 6). Alert, unlike pup checking, did not vary throughout lactation; therefore, despite pup activity positively influencing this behaviour in step 2 and step 3 of the analyses, there was no evidence from any of the analyses that the age of the pup influenced this behaviour too. However, the diurnal analyses of the NSA data did show that

females were more alert during the early hours of the day (Chapter 3, Section 3.7.2). Similar diurnal patterns (whereby individuals are more alert at first light) have been shown in male grey seals too (Anderson, 1978; Twiss, 1991). Therefore, when visibility increases (increased daylight), individuals are initially more alert. The influence of daylight on this behaviour has also been shown in night-time observations of grey seals during the breeding season, which found that individuals spent significantly less time alert during the night-time than the day-time (Culloch et al., unpublished data). Consequently, the alert behaviour may be an indication of how aware an individual is of their surroundings, and/or an indication of how 'nervous' they are. Therefore, although alert and pup checking may appear to be similar behaviours, the pup checking behaviour is mainly directed at monitoring the status and/or location of the pup, whereas the alert behaviour is related to monitoring the individuals' broader surroundings. Consequently, these comparisons suggest that these are functionally different behaviours.

9.3.1. Fitness consequences of CIDs in behaviour: the adaptive hypothesis

There has been much debate on whether or not (and to what extent) CIDs in behaviour are adaptive or are a product of (phenotypic and/or genotypic) constraints (e.g. DeWitt et al., 1998; Dall, 2004; Dingemanse & Réale, 2005; Chapter 1, Section 1.5). In the present study, there was no evidence that the pup check or alert behaviour influenced pup daily growth rate (PDGR) or the mass transfer efficiency (MTE; Chapter 8). However, it may be that the fitness benefits of CIDs in behaviour are not related to these commonly used short-term proxies of fitness, rather, they could be related to pup survival. For example, in sheep, low levels of maternal vigilance contribute to weaker bonds with offspring, which in turn have higher mortality rates (Dwyer, 2008). Therefore, over their lifetime, mothers that are more alert may successfully raise more pups to weaning, compared to their less alert counterparts.

On the breeding colony, pup mortality is highest in the first few days postpartum, with starvation and infection being the main causes of death (which typically occurs as a result of the mother-pup bond not forming or being broken,

Anderson et al., 1979; Baker, 1988). Furthermore, although there are no terrestrial predators on island breeding colonies in the U.K., greater and lesser black-back gulls (*Larus marinus* and *L. fuscus*, respectively) are known to attack weakened and/or unprotected pups (Twiss et al., 2003; Culloch et al., 2012). Therefore, coupled with potential threats from conspecifics (e.g. pups being crushed; Anderson et al., 1979), increasing the proportion of time spent pup checking and/or alert, particularly at the early stages of lactation, could increase the likelihood of pup survival. The exploratory analyses showed that mothers did spend more time pup checking during early lactation; however, as was noted in Section 9.3, pup age was omitted from steps 2 or 3 of the analyses for the NSA datasets (due to consistent collinearity). For the alert behaviour, which did not vary significantly throughout lactation, factors other than pup age may have influenced this behaviour later in lactation; for example, an increase in the number of approaches by males as the female approaches oestrous (Twiss, 1991; Pomeroy et al., 1999). Consequently, this could explain how the proportion of time spent alert was maintained throughout lactation.

Twiss et al. (2003) suggested that the habitat quality (Twiss et al., 2000) and the influence of the pup-pool trade-off (Redman et al., 2001) could be important factors in determining whether or not gulls attacked pups. They hypothesised that females that pup further from pools (and therefore in lower quality habitat) would spend more time further away from their pup (because they spend more time commuting between pup and pool), which in turn, would make their pup more vulnerable to attacks by gulls. Unfortunately, links between CIDs and the likelihood of the pup dying could not be tested in the present study, because all females raised their pup to weaning, and were therefore 'successful' mothers. Irrespective, mothers without pups (either not pregnant or whose pup had died) could not be included in these analyses because the behavioural context for these females would have been different to those with pups. Moreover, other than the pup being dead or alive (which is a rather coarse metric) there would have been no proxies of short-term fitness for females without a pup.

Female grey seals are known to breed from 4 through to 42 years of age (Pomeroy et al., 1999; Bowen et al., 2006). Therefore, the data presented in

Chapter 8 are arguably a brief insight into a mother's pupping success, which may not be representative of her reproductive output over her lifetime, particularly since inter-annual variation in reproductive expenditure has been shown to occur in female grey seals (Pomeroy et al., 1999; Bowen et al., 2006). An alternative approach to assess whether or not CIDs in alert and/or pup checking do have fitness consequences, with respect to pup survival, would be to compare the number of pups successfully raised to weaning throughout an individual's lifetime. However, if a relationship were shown, this would raise the question of why are all females not more alert (and/or why do all females not spend more time pup checking), if this strategy results in successfully raising more pups to weaning. One explanation could be that there is a considerable fitness cost to the mother (e.g. increased probability of mortality; Section 9.4.2, below). Nevertheless, this analytical approach would also allow the inclusion of females that were unsuccessful (i.e. did not give birth or their pup died; assuming that a 'behavioural type' could be assessed across breeding seasons where they did successfully wean a pup).

There are a growing number of theoretical studies that consider state-dependency to be a potential explanation for the occurrence of CIDs in behaviour (Dall et al., 2004; McElreath & Strimling, 2006; Stamps, 2007; Biro & Stamps, 2008; Carere et al., 2010); however, few have attempted to quantify this (Mathot et al., 2011; Section 9.4.2, below). In the present study, there was no relationship between the pup check or the alert behavioural category with any of the reproductive covariates in either of the two breeding seasons. However, compared to the data used in the preliminary analyses presented here, the long-term, longitudinal dataset for North Rona (which spans five decades) does contain additional data pertaining to other aspects of known individuals' life-history. Therefore, these data can provide additional important information on underlying differences in individuals' state (e.g. body length, health of individual, age; that were not used in this study), which could be used to empirically address whether or not CIDs in behaviour are influenced by state-dependent factors.

9.3.2. Neutral variation: the non-selective hypothesis

The preliminary findings presented in this thesis suggest that CIDs in behaviour do not influence commonly used proxies for short-term fitness. It is therefore, important to consider the possibility that natural selection does not distinguish between alternative behavioural responses to variation in social and/or environmental conditions. As a result, these alternative responses could simply represent random, non-adaptive, neutral variation (Carere et al., 2010) that does little or nothing to improve an individual's fitness whilst on the breeding colony.

As a capital breeder, female grey seals must sustain the energetically demanding period of lactation while fasting, relying on body energy stores (in the form of blubber) for maintenance metabolism and milk production (Mellish et al., 1999; Pomeroy et al., 1999; Iverson et al., 2003; Bowen et al., 2006). As both pup check and alert are likely to be low energy behaviours, and do not contribute substantially to an individual's energy budget, it could therefore be possible that no selective pressure is acting on these behaviours. There are few studies that have attempted to calculate the contribution of different behavioural components to an individual's overall energy budget in free-living, wild animals. Of those that have, a recent study on king penguins (*Aptenodytes patagonicus*) used heart rate-loggers (which can be used to estimate energy expenditure) to show that incubating birds spent up to 22% of their time budget in 'comfort' behaviour, which equated to ca. 9% of their total energy budget (Viblanc et al., 2011). Therefore, advances in these approaches means that it is possible to quantitatively assess the energy budget of grey seals, and determine whether or not pup check and alert are low energy behaviours. If these behaviours do comprise only a small proportion of an individual's energy budget, then this could add to the supposition that the CIDs in the pup check and the alert behaviours are simply just random, non-adaptive, neutral variation that has no consequence to an individual's fitness. However, irrespective of the energy investment (not considering the resting behavioural category), alert comprises a large proportion of an individual's activity budget (Chapter 3, Table 3.1), so even if this behaviour is low energy, it does nevertheless, raise further questions about the impact on the expression of other behaviours that may not be neutrally selected.

9.3.3. Are CIDs in behaviour context specific?

Several studies have shown that CIDs in behaviour across contexts might result in ecologically important behaviours appearing to be neutral or maladaptive in an isolated context (Wilson et al., 1993; Sih et al., 2003; van Oers et al., 2005; Martin & Réale, 2008a). For example, Johnson & Sih (2005) showed that precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*) represented a spillover of aggression across both ontogeny (juvenile-adult) and behavioural contexts (foraging – mating – anti-predator). Other studies have shown that larval salamanders (*Ambystoma barbouri*) display high activity in the presence and absence of predators. In the latter scenario individuals acquired more resources and developed faster, but in the former the same individuals took considerably greater risks in the presence of predators (Sih et al., 2003). These examples clearly highlight the need to look across contexts when studying the causes and consequences of CIDs in behaviour.

In the present study, in the context of the breeding season, there may be no selective advantage to being more or less alert and/or spending more or less time pup checking. However, these behaviours, and in particular, alert, may be important in other contexts, such as foraging whilst at sea. Consequently, it would be of particular interest to follow a range of 'behavioural types' at sea, to assess whether home range patterns (McConnell et al., 1999; Wolf & Trillmich, 2007; Lowther et al., 2011), dive patterns (Burns et al., 2008) and diet (Tucker et al., 2007; Newland et al., 2009; Lowther et al., 2010) are related to these CIDs in the alert behaviour. If such studies identified CIDs in behaviour at sea, then this could lead to further studies to identify genes or genome regions that underlie CIDs in behaviour, in an effort to understand natural selection at the molecular level (Bell & Vubin-Horth, 2010; van Oers & Muller, 2010; Elmer & Meyer, 2011) and to gain a greater insight into how an individual's genotype and phenotype interacts with the environment (Dingemanse et al., 2004; Nussey et al., 2007b).

9.4. Potential mechanisms that maintain CIDs

9.4.1. The influence of social and environmental factors on development

There are a wealth of studies on a number of species, which have shown that social and/or environmental factors during early phases of life do influence the behaviour of individuals (Gotz & Stefanski, 2007; Nussey et al., 2007b; Mueller et al., 2011) and, in the context of CIDs in behaviour, this has been discussed recently in a number of reviews (Stamps & Groothuis 2010a, b; Groothuis & Trillmich, 2011; Siegler, et al., 2011; Trillmich & Hudson, 2011). This early developmental period, which coincides with the time of parental dependence, is important for the offspring in fine-tuning its phenotype to the current environmental conditions (Stamps, 2003), which can be influenced by the parents (Crews & Groothuis, 2005). For example, guinea pig (*Cavia aperea f. porcellus*) pups that spend longer periods of time apart from their mother have been shown to be more exploratory (Albers et al., 2000). In the context of the present study, given that maternal attendance is heavily influenced by environmental factors (e.g. access to pools, rainfall and air temperature) that were shown to vary considerably between breeding seasons (Chapter 3, Section 3.14), this does raise interesting questions with respect to whether or not (and to what extent) environmental variation coupled with the mothers' behaviour is (directly or indirectly) influencing their pups' behavioural phenotype.

9.4.2. Life-history traits and frequency dependence

Using a theoretical approach, Wolf et al. (2007) explained how CIDs in behaviour could be maintained by life-history trade-offs. They compared individuals that explored their environment thoroughly with superficial explorers. They found that the latter evolved high levels of aggression and were bolder, whereas the opposite was true for the former. Furthermore, they included a quantitative genetic component to their model to show that these CIDs in behaviour could, theoretically, evolve and remain stable (Wolf et al., 2007). As mentioned in Chapter 1 (Section 1.5), Stamps (2007) and Biro & Stamps (2008) consider the trade-off between increased growth resulting in a greater probability

of mortality due to an increase in mean levels of potentially risky behaviour across populations. Therefore, within populations, the faster growing individuals will take more risks in foraging contexts than the slower growing individuals, and, as a consequence, the former will suffer an increased probability of mortality.

Previous studies on grey seals have shown that females with a greater maternal mass at parturition produce heavier pups at weaning (Anderson & Fedak, 1987; Iverson et al., 1993; Pomeroy et al., 1999). If the alert (or pup check) behaviour did relate to behaviours at sea, such as bold and exploratory, and if these individuals gained a fitness benefit of increased annual growth, then these more alert females would produce heavier pups at weaning, which are more likely to survive into their first year (Hall et al., 2001). However, as a consequence, these females may suffer an increased probability of mortality as a result of early reproduction (Bowen et al., 2006; Nussey et al., 2006; Nussey et al., 2008) and/or through risky foraging behaviour required in order to maintain continually high energy demands (e.g. incidental bycatch; Bjorge et al., 2002; Backlin et al., 2011). Conversely, females that are less alert may be less exploratory, more shy and risk averse, they may also reach sexual maturity at an older age. Consequently, this life-history strategy would reduce the probability of mortality and thus offers an explanation as to how CIDs in the alert behaviour could persist, and remain stable within a population (Stamps, 2007; Wolf et al., 2007; Biro & Stamps, 2008). However, this may not offer an entirely satisfactory explanation given that the analyses presented in Chapter 8 found no relationship with alert (or pup check) and the maternal postpartum mass, which would be expected under this hypothesis. It is possible that the failure to identify a relationship between these behaviours and the maternal postpartum mass could be attributed to the relatively small sample size of individuals (and of breeding seasons), or that maternal postpartum mass is not a sufficiently accurate proxy of condition or length (Pomeroy et al., 1999; Hall et al., 2001).

Although there are many theoretical approaches to explaining the existence and the fitness trade-offs of CIDs in behaviour, there are very few studies that have provided empirical support for these hypotheses. Of the empirical studies that do exist, Mathot et al. (2011) carried out a series of experiments in which they

manipulated the perceived predation danger for red knots (*Calidris canutus islandica*). They found that vigilance, which had a negative frequency-dependent payoff, was consistent across repeated observations of the same individuals. Conversely, for escape flights, which had a positive frequency-dependent payoff, all individuals within the flocks had similar responses; therefore, almost all of the variation in this behaviour was explained by the group, and not the individual. Furthermore, they found no evidence to suggest that vigilance was state-dependent. Therefore, Mathot et al. (2011) provide evidence that negative frequency-dependency did explain variation in plasticity; however, they acknowledged that negative frequency-dependence is not a sufficient explanation as to why individuals should differ consistently in their behaviour. In another example, Dingemanse et al. (2004) showed that direction of selection on exploratory tendency of great tits (*Parus major*) changed from year to year in relation to food availability. They hypothesised that these fluctuations in food availability will lead to fluctuations in competition for other resources, which could drive selection pressure and ultimately explain how CIDs in behaviour can be maintained in a fluctuating environment. Consequently, if individuals are not completely flexible in their behaviour, and if the local spatio-temporal conditions fluctuate unpredictably, then selection could potentially preserve a mixture of these 'behavioural types'. In the marine environment, these fluctuating and/or unpredictable environments are often reported to influence the distribution and/or foraging behaviour of marine predators (e.g. Friedlaender et al., 2006; Tetley et al., 2008; Mueller et al., 2011). Therefore, grey seals are also likely to experience these fluctuating and/or unpredictable conditions whilst foraging at sea, which could explain the occurrence of CIDs in the alert behaviour, if they were adaptive in this context.

9.4.3. Coping with a fluctuating environment

Based on the manner in which individuals handle environmental and social challenges, previous studies have described two 'coping styles', referred to as proactive and reactive (Koolhaas et al., 1999). In rodents, aggressive males have a more proactive type of behavioural response, whereas non-aggressive or reactive males seem to be more adaptive and flexible, responding when absolutely

necessary (Benus et al., 1991; Koolhass et al., 1999). Similarly, in birds, individuals that are quick to explore their environment are proactive, whereas those that are slow are reactive (Carere et al., 2005). Therefore, in a stable environment, high levels of aggression in mice, or fast exploration in birds is the best strategy; conversely, in a variable and/or unpredictable environment, lower levels of aggression, or slow exploration is the best strategy (Koolhaas et al., 1999). In the present study, with the exception of the activity of the pup, there was limited evidence that social and/or environmental variation on the breeding colony influenced the pup check or the alert behaviour in steps 2 or 3 of the analyses (Chapters 5, 6 and 7). Although the influence of collinearity cannot be ruled out, no covariate was consistently collinear with pup activity, which was the most influential covariate for both behaviours. It is also possible that a significant relationship between the alert (and/or pup check) behaviour and the proactive-reactive 'coping styles' does occur; however, it may be that they are context specific (e.g. foraging; Section 9.4.2).

9.4.4. Conservation and management implications

Whatever the causes, CIDs in behaviour do have important implications for conservation and management. This is especially true for grey seals in the U.K., which do breed on a variety of terrain, from sandy beaches (e.g. Monach Islands, Donna Nook; Harwood, 1976), flat low rock (e.g. Isle of May; Pomeroy et al., 2000a; Twiss et al., 2001) and open, boulder strewn, grass (e.g. North Rona; Pomeroy et al., 1994; Twiss et al., 1994). Some of the breeding colonies around the U.K. are prone to anthropogenic (tourists) and/or natural (tides) disturbance. This diversity in both terrain and levels (and causes of) disturbance does raise an interesting question as to whether or not these CIDs in behaviour also exist on other colonies, especially since North Rona (and in particular the NSA) were relatively undisturbed. This may be particularly important to consider with respects to tourism as previous studies have shown that behavioural changes do occur in animals that have been affected in some way by human interactions such as direct human contact, disturbance and/or encroachment (Anthony & Blumstein, 2000; Louis & Le Beere, 2000; Lacy & Martins, 2003). For example, in Eastern chipmunks (*Tamias striatus*) the distribution patterns of certain types of individual

is heavily influenced by the presence of humans (Martin & Réale, 2008a) and in yellow-eyed penguins (*Megadyptes antipodes*), when humans are in close proximity, certain types of individual experience a significant increase in heart rate with long recovery times, which causes unnecessary physiological stress and increased energy expenditure (Ellenberg et al., 2006; Ellenberg et al., 2007; Ellenberg et al., 2009). Therefore, these studies illustrate that certain types of individual do not habituate to human presence. In the case of grey seals, this may have important implications for colonisation patterns and reproductive success, especially on breeding colonies such as Donna Nook, which, on average, is visited by more than 1,300 tourists per weekend (Rob Lidstone-Scott, Lincolnshire Wildlife Trust, pers. comm.).

9.4.5. Marine mammals; a more general overview

More broadly, it is apparent that marine mammals in general are underrepresented in this field of evolutionary and behavioural ecology, with only three studies attempting to explicitly quantify CIDs in behaviour (Highfill & Kuczaj, 2007; Twiss & Franklin, 2010; Twiss et al., 2011a). However, there are a substantial number of studies covering a broad range of marine mammal species, which have shown that individual variation does occur in: diet and foraging specialisations (e.g. Cherel et al., 2007; Foote et al., 2009; Newsome et al., 2009), habitat use and site fidelity (e.g. Deutsch et al., 2003; Hoffman et al., 2006; Wolf & Trillmich, 2007), vocalisation (e.g. Sousa-Lima et al., 2002; Antunes et al., 2011; Trimble & Charrier, 2011), pathogen infection rates (e.g. Johnson et al., 2009), display behaviours (e.g. van Parijs et al., 2000) and proxies of short- and long-term fitness (e.g. Pomeroy et al., 1999; Bowen et al., 2006; McDonald et al., 2009).

Of these, foraging specialisations are perhaps more prominent in the literature. One of the most detailed studies on this behaviour is on sea otters (*Enhydra lutris*), which are renowned for their diverse diet (Estes et al., 2003; Tinker et al., 2007; Tinker et al., 2008; Newsome et al., 2009). However, several studies have shown that individuals tend to specialise on 1 - 4 prey types (Estes et al., 2003; Tinker et al., 2008) with little variation occurring in an individual's diet

over time (Estes et al., 2003; Tinker et al., 2007; Newsome et al., 2009). This lack of individual variation is thought to be a result of foraging behaviours being learnt during maternal dependence (Estes et al., 2003). Subsequently, the costs of phenotypic plasticity associated with acquiring the specialist skills required to successfully utilise a different prey type could explain why such low within-individual variation in the diet exists within this population. Furthermore, these studies have shown that, in resource-limited environments, individual's benefit from dietary specialisation through more efficient prey handling (Tinker et al., 2008). Equivalent studies on grey seals are lacking; however, at the population-level, studies from Sable Island, Canada have shown that adult males tend to feed on more benthic prey, whereas juveniles and adult females tend to feed on more pelagic prey (Tucker et al., 2007). Again, such studies argue strongly for the need to extend the study of CIDs in the behaviour of grey seals out to sea.

9.5. Conclusion

This thesis has shown that CIDs in behaviour, and in particular, the alert behaviour, do occur in wild postpartum female grey seals. There are a number of potential explanations for this, which have been discussed above. However, without further studies, it is not possible to state which of these hypotheses are responsible for maintaining CIDs in these behaviours. Nevertheless, broadly speaking, there are two important considerations for future studies on CIDs in the behaviour of wild animals *in situ*: 1) the need for long-term, longitudinal datasets and 2) the need to investigate CIDs in behaviour across contexts. With respect to the first point, in order to identify the ecological and evolutionary significance of individual variation in behaviour, previous studies have shown that long-term longitudinal datasets are exceptionally important (e.g. Nussey et al., 2005a, b; Moyes et al., 2009; Wilson et al., 2009). Furthermore, without these datasets it would not be possible to ascertain at which life-stage(s) selection pressure primarily acts on CIDs in behaviour or if CIDs in behaviour are maintained throughout an individual's lifetime (Stamps & Groothuis, 2010a, b; Groothuis & Trillmich, 2011). Similarly, for the second point, several studies have illustrated the importance of investigating whether or not CIDs in behaviour occur across contexts. Consequently, these studies have not only provided further insights in to

the ecological and evolutionary significance of CIDs in behaviour, but they have also shown that it is important to consider behaviour in a more holistic way (rather than the 'traditional' approach of studying behavioural contexts independent of one another; Wilson et al., 1993; Sih et al., 2003; Johnson & Sih, 2005; Bell, 2007).

Following the general guidelines presented in this chapter, the three-step analytical process can be applied to data collected on other species. With respect to marine mammals, there are few studies on CIDs in behaviour, despite the fact that many researchers are often working with their study species at the individual-level. Therefore, it is suspected that many peers will have datasets to which this novel three-step analytical approach can be applied, in order to ascertain whether or not CIDs in behaviour do occur in their study species. Furthermore, this approach is not limited to observational data, it could be applied to dive data, foraging data, and other contextual behaviours. From this perspective, this analytical approach offers a novel insight in to CIDs in behaviour, across a broad range of situations and contexts.

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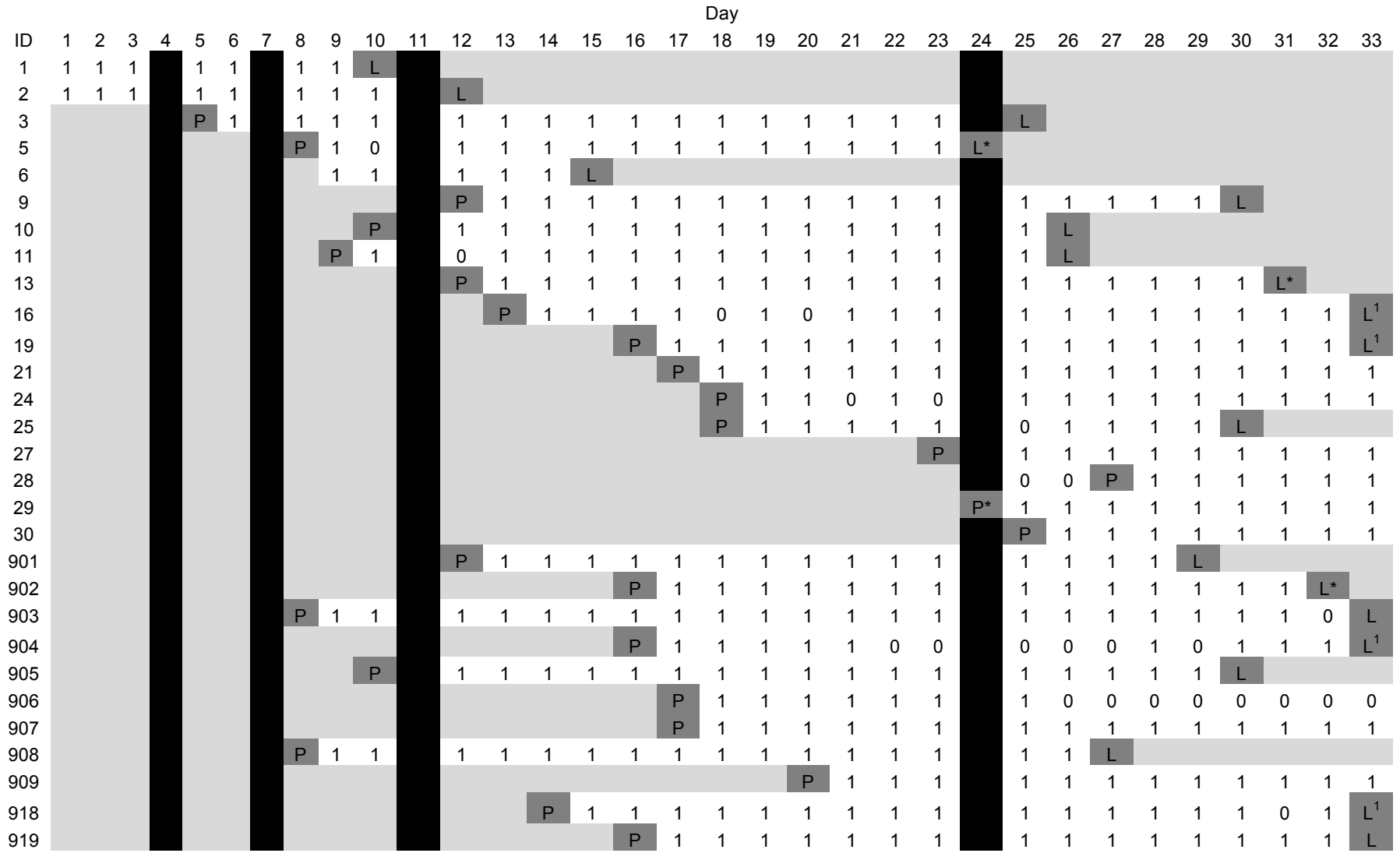
Chapter 3: Appendix

The follow three pages show:

Tables **A3.1**, **A3.2** and **A3.3:** The presence and absence data for each of the individual postpartum female grey seals that were included in the data analyses for the 2007, 2008 and 2009 breeding seasons, respectively. Day 1 in all three years is 30th September. The unique individual identification code is shown in the ID column; IDs < 900 were seen in only one breeding season; IDs > 900 were seen in two or more breeding seasons. '1' indicates the female was seen on that day; '0' indicates that the female was not seen on that day; the day the female gave birth is shown as a 'P' in a dark grey cell; the day the female left the colony is shown as an 'L' in a dark grey cell; * indicates that the date of birth/leaving date is an estimate; L^1 indicates that the female was not seen during a presence/absence survey on the last day on North Rona and was therefore assumed to have left; light grey cells are used to indicate that observational data were not collected (e.g. if the female was pregnant or if the female had left the colony); black cells are used to indicate days in which data were not collected; in 2007 data were not collected on days 4, 7, 11 or 24 due to assisting with other field studies; in 2008 data were not collected on day 26 due to unsafe weather conditions.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2 1 1 1 1 1 1 1 L
3 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
5 P 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L*
6 1 1 1 1 1 L
9 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
10 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
11 P 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
13 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L*
16 P 1 1 1 1 0 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L1
19 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L1
21 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
24 P 1 1 0 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
25 P 1 1 1 1 1 0 1 1 1 1 L
27 P 1 1 1 1 1 1 1 1 1 1
28 0 0 P 1 1 1 1 1 1
29 P* 1 1 1 1 1 1 1 1 1
30 P 1 1 1 1 1 1 1 1
901 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
902 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L*
903 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 L
904 P 1 1 1 1 1 0 0 0 0 0 1 0 1 1 1 L1
905 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
906 P 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0
907 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
908 P 1 1 1 1 1 1 1 1 1 1 1 1 1 L
909 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
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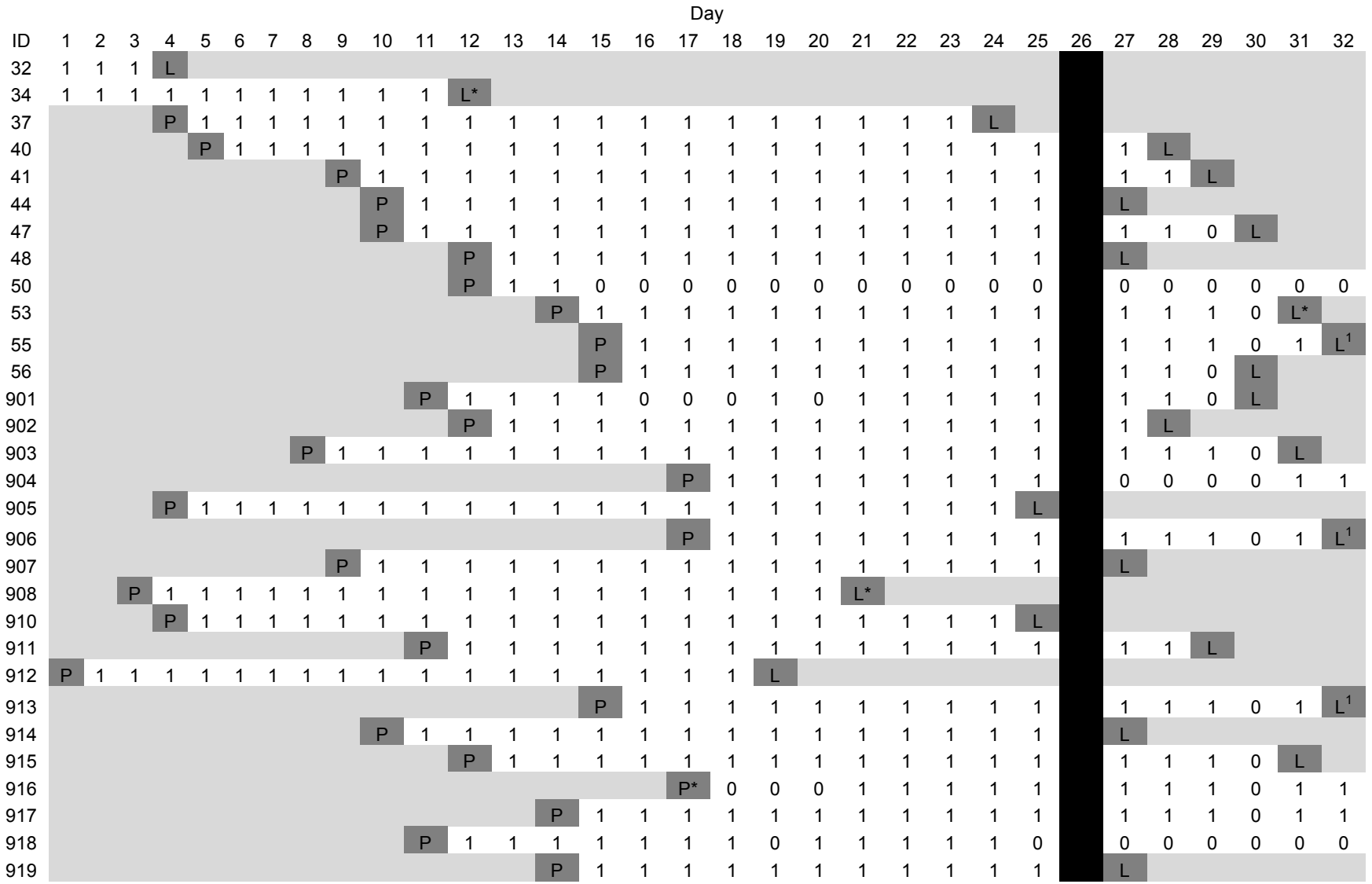
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32 1 1 1 L
34 1 1 1 1 1 1 1 1 1 1 1 L*
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48 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
50 P 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
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56 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 L
901 P 1 1 1 1 0 0 0 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 0 L
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903 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 L
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905 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
906 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 1 L1
907 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
908 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L*
910 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
911 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
912 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
913 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 1 L1
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915 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 L
916 P* 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0
917 P 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0
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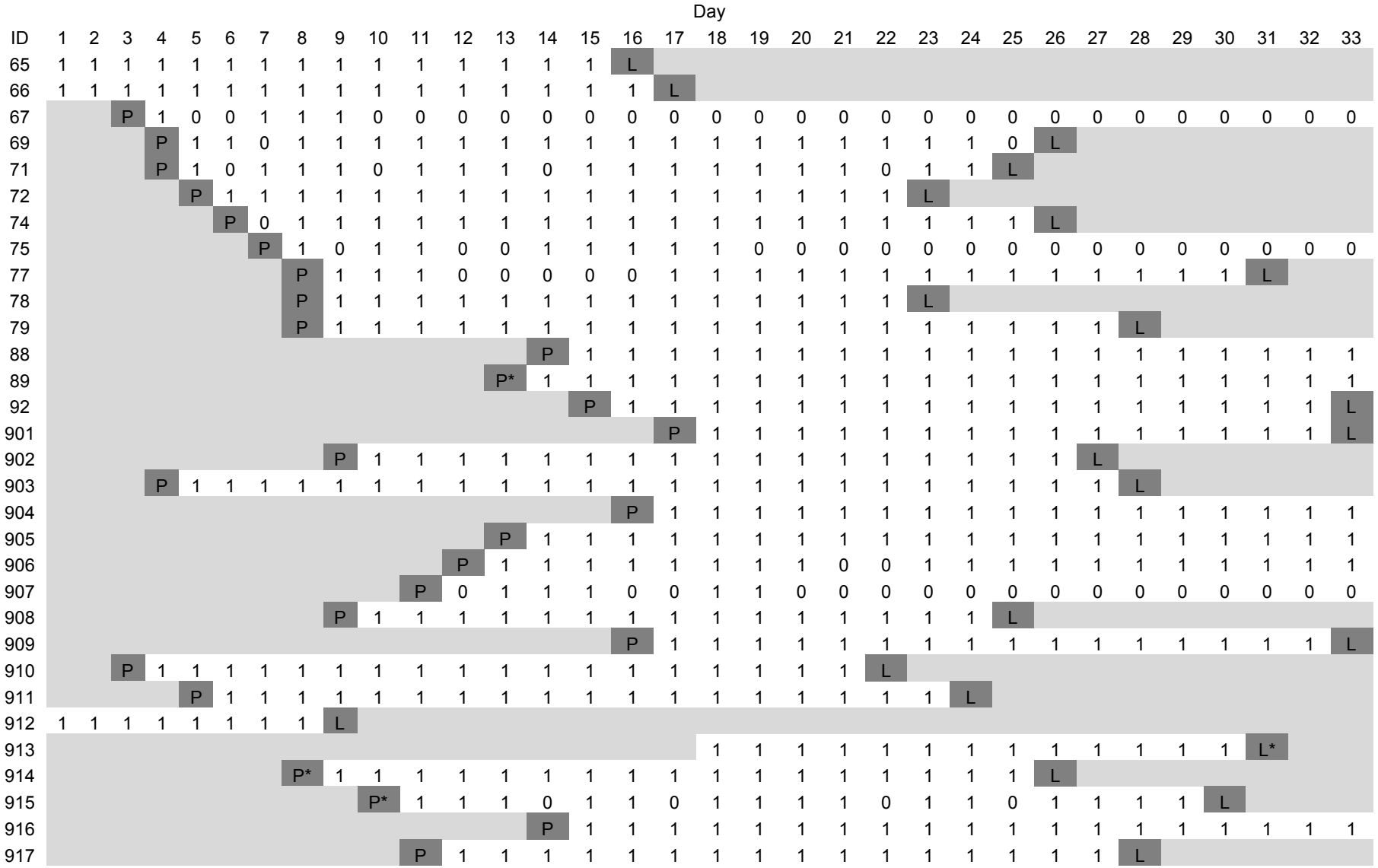
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66 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 L
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912 1 1 1 1 1 1 1 1 L
913 1 1 1 1 1 1 1 1 1 1 1 1 1 L*
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915 P* 1 1 1 0 1 1 0 1 1 1 1 0 1 1 0 1 1 1 1 L
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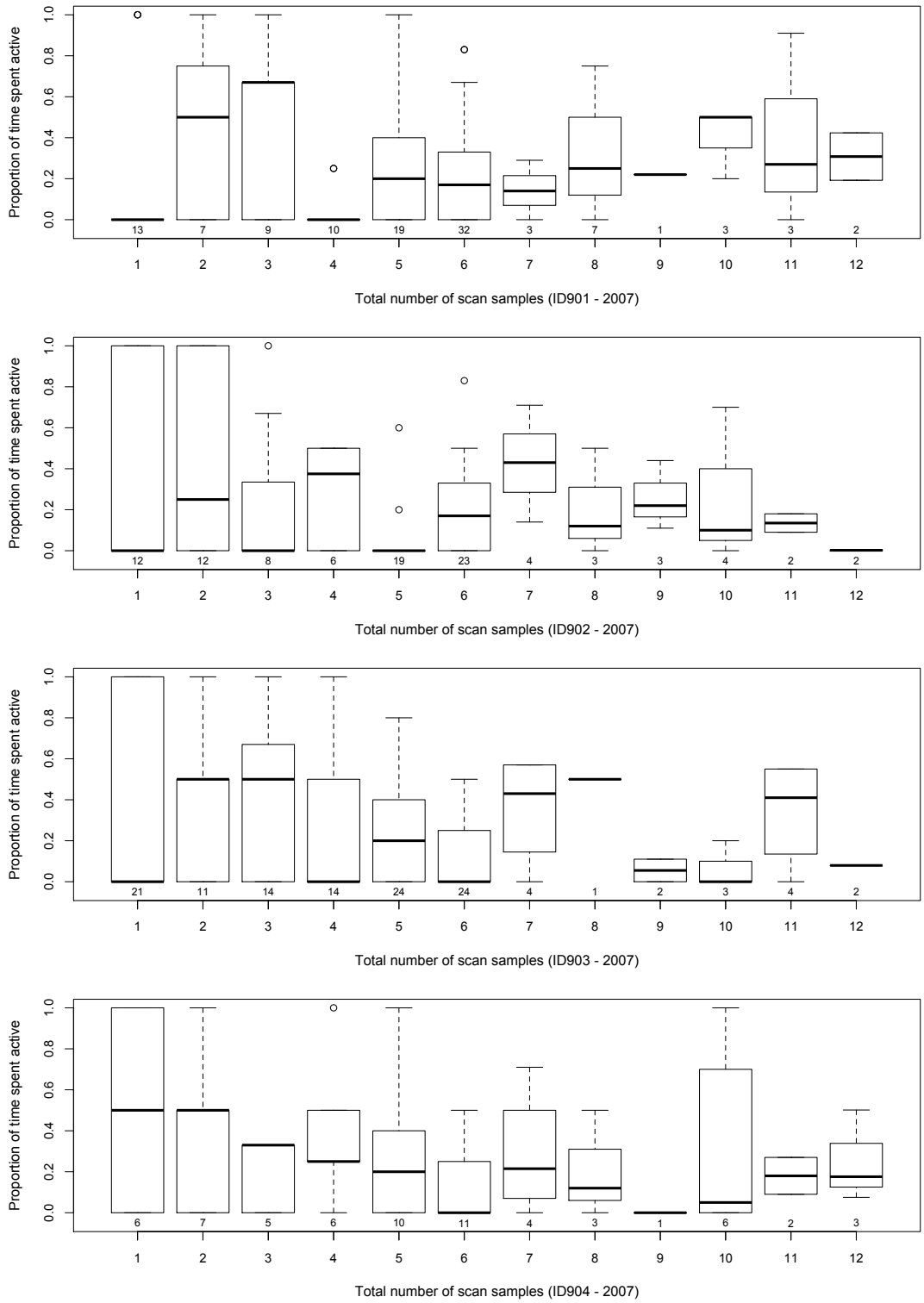


Figure A3.1: A subset of the individual activity plots of pups of re-sighted females plotted against the total number of scan samples collected per hour for the 2007 breeding season. The number of samples collected for each of the 'total number of scan samples' is noted on the inside of the x-axis. The female's ID code is shown on the x-axis (e.g. ID901) with the year.

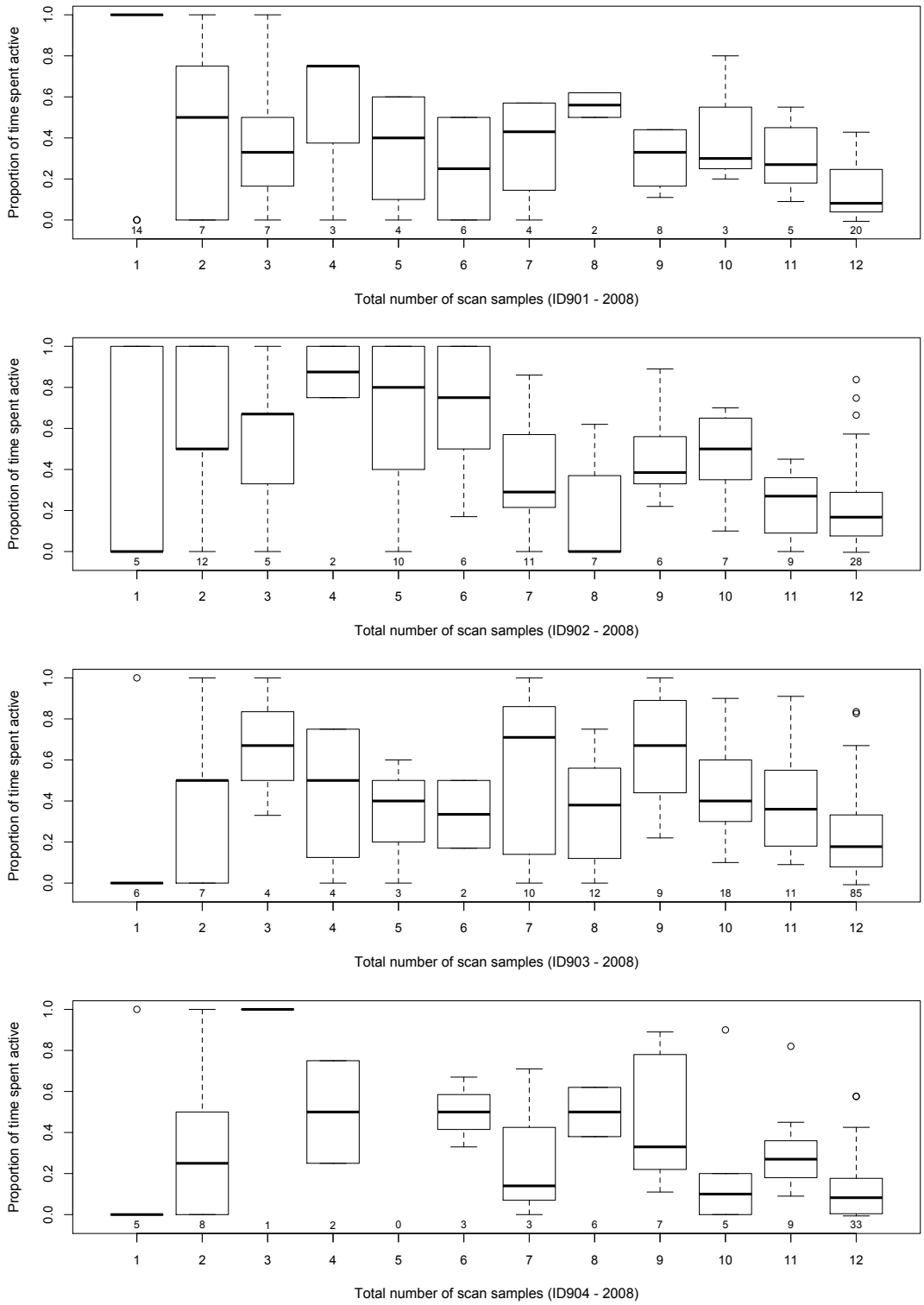


Figure A3.2: A subset of the individual activity plots of pups of re-sighted females plotted against the total number of scan samples collected per hour for the 2008 breeding season. The number of samples collected for each of the 'total number of scan samples' is noted on the inside of the x-axis. The female's ID code is shown on the x-axis (e.g. ID901) with the year.

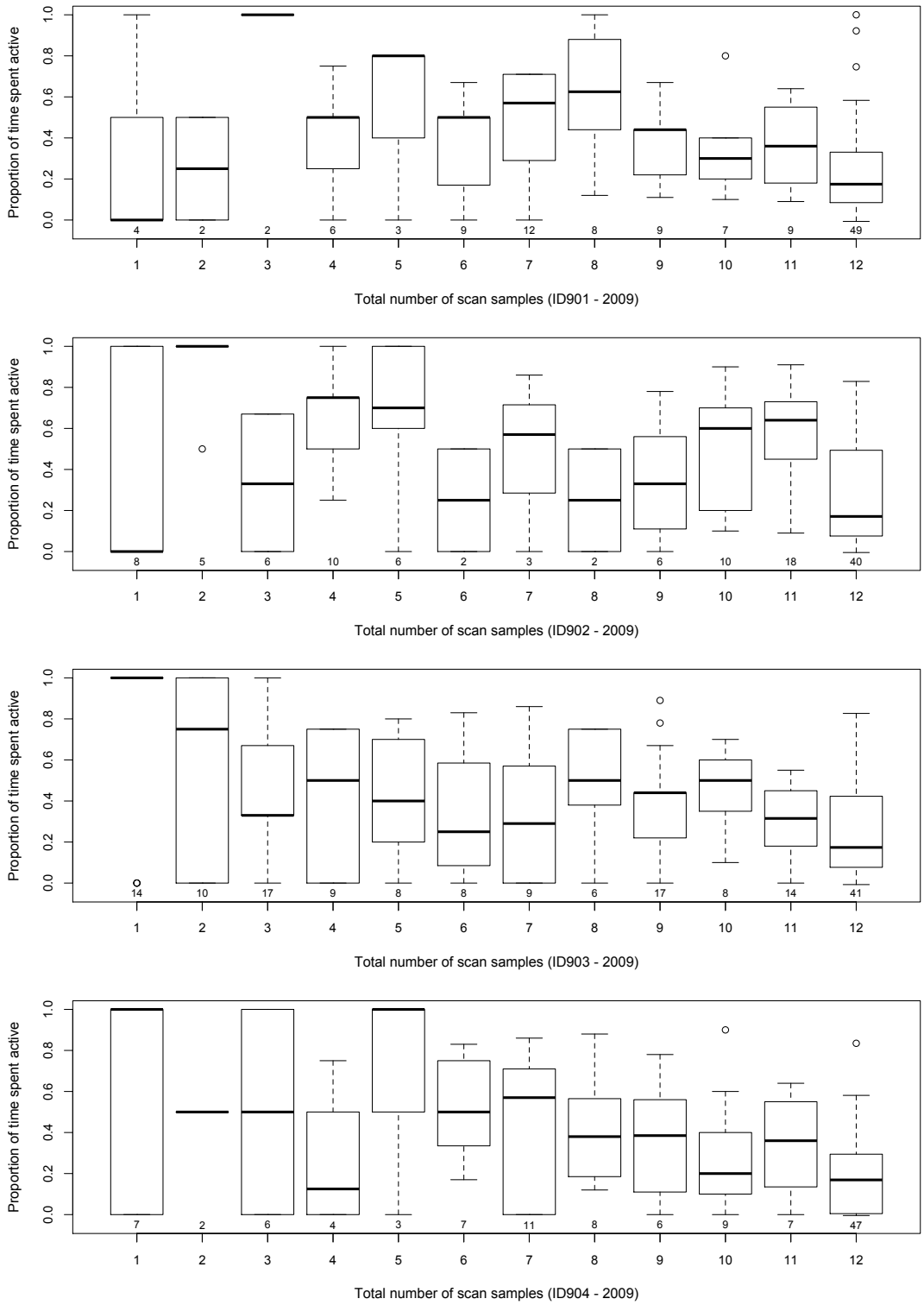
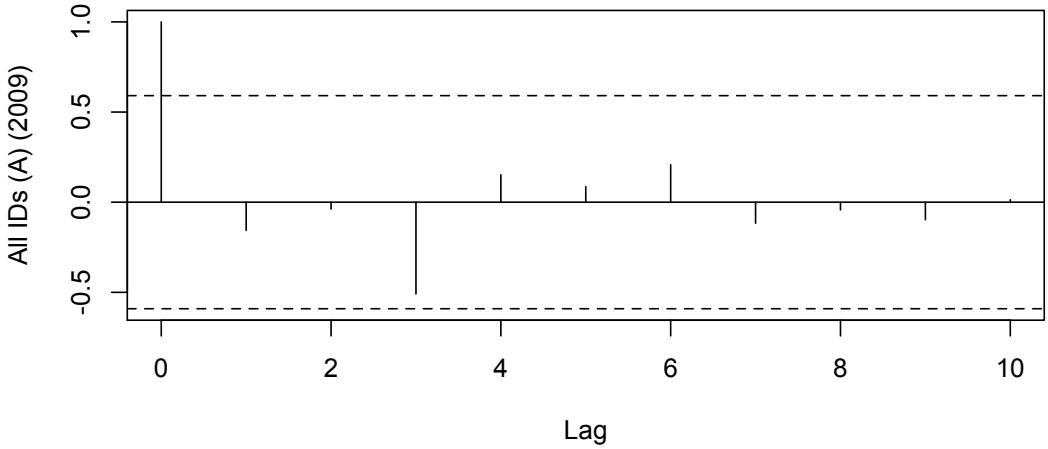


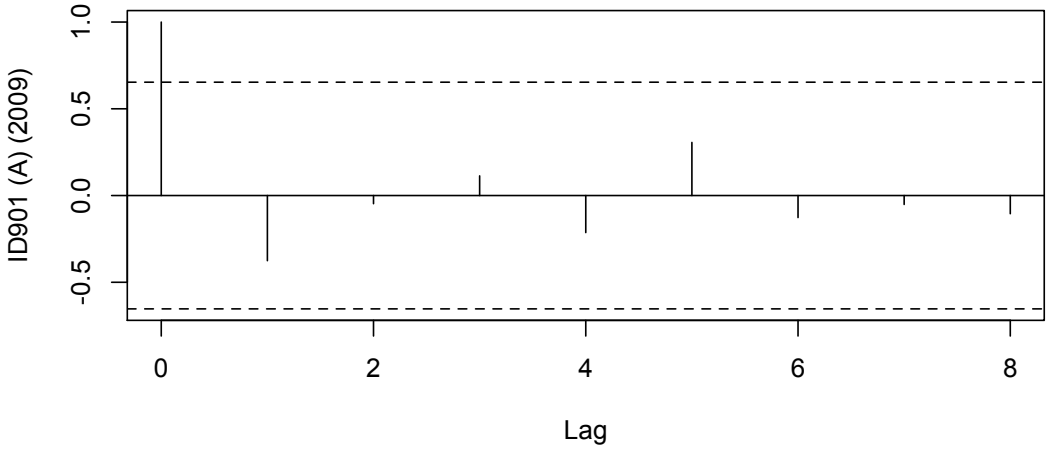
Figure A3.3: A subset of the individual activity plots of pups of re-sighted females plotted against the total number of scan samples collected per hour for the 2009 breeding season. The number of samples collected for each of the 'total number of scan samples' is noted on the inside of the x-axis. The female's ID code is shown on the x-axis (e.g. ID901) with the year.

Figure A3.4: A subset of the autocorrelation function (ACF) plots. The ACF plots shown here are for the alert behavioural category for **a)** all individuals and for **b - h)** a selection of individuals (unique ID code is shown on the y-axis) from the 2009 breeding season. All ACF plots are from the alert (A) behavioural category. The hour-to-hour lag points are shown on the x-axis and the dashed black horizontal line shows the 95% confidence interval. Note that the autocorrelation at lag 0 is included and always takes the value of 1, as it represents the correlation between the data and themselves. Autocorrelation occurs if the data (vertical line) crosses the 95% confidence interval. There are a maximum of 10 lags (for a total of 11 hours); however, some females have fewer lags because data were not collected in a given hour (most likely the first and/or last hour of the day).

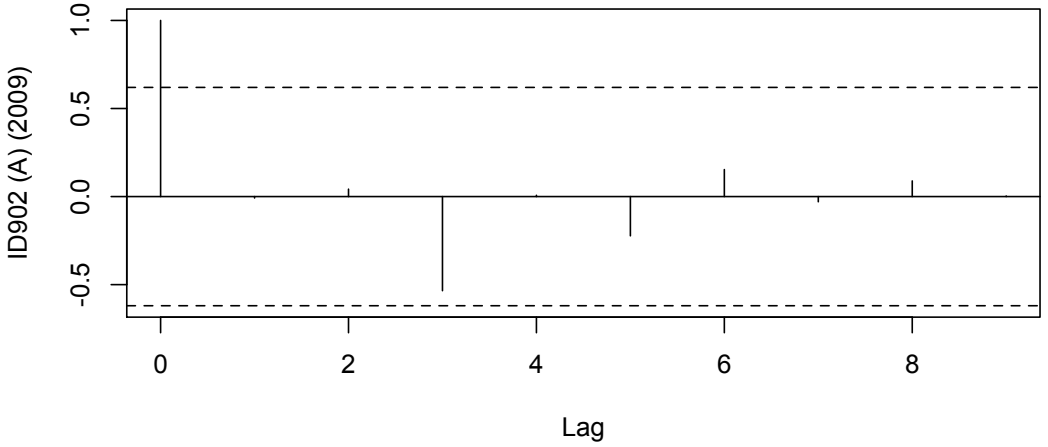
a)


All IDs (A) (2009)
1.0
0.5
0.0
-0.5
0
2
4
6
8
10
Lag

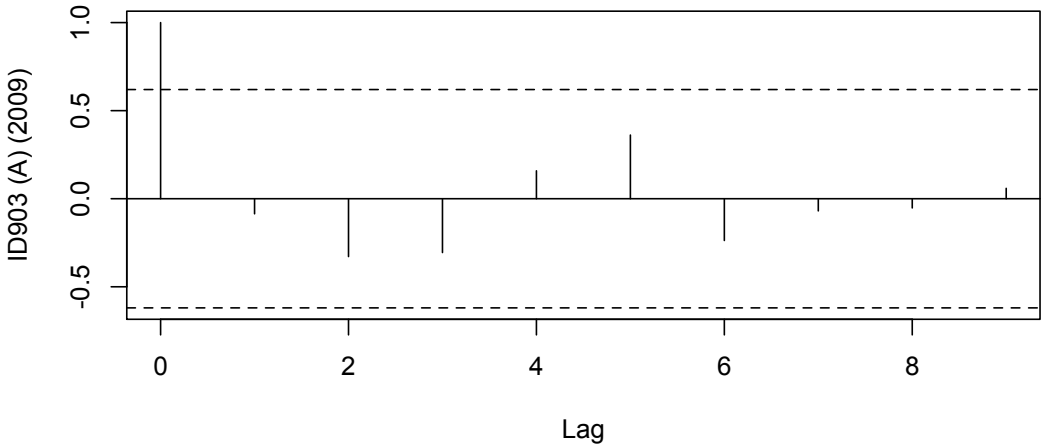
b)


ID901 (A) (2009)
1.0
0.5
0.0
-0.5
0
2
4
6
8
Lag

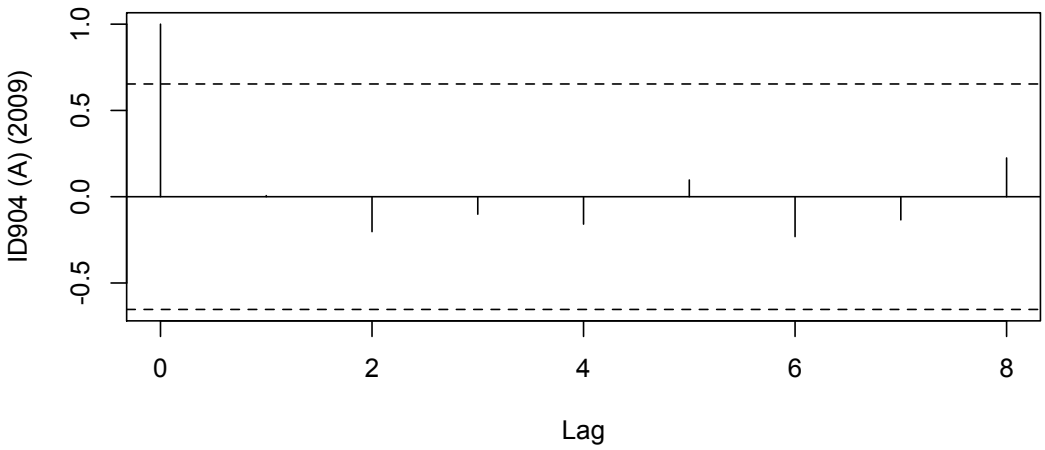
c)


ID902 (A) (2009)
1.0
0.5
0.0
-0.5
0
2
4
6
8
Lag

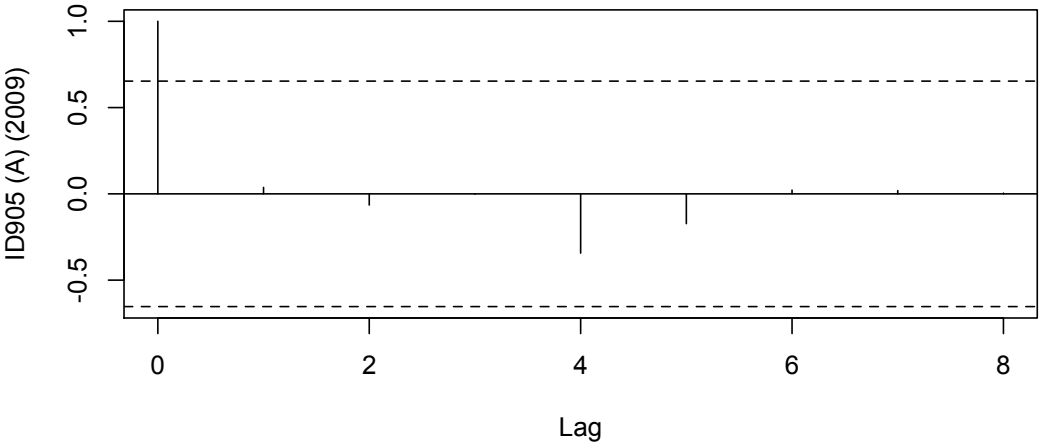
d)


ID903 (A) (2009)
1.0
0.5
0.0
-0.5
0
2
4
6
8
Lag

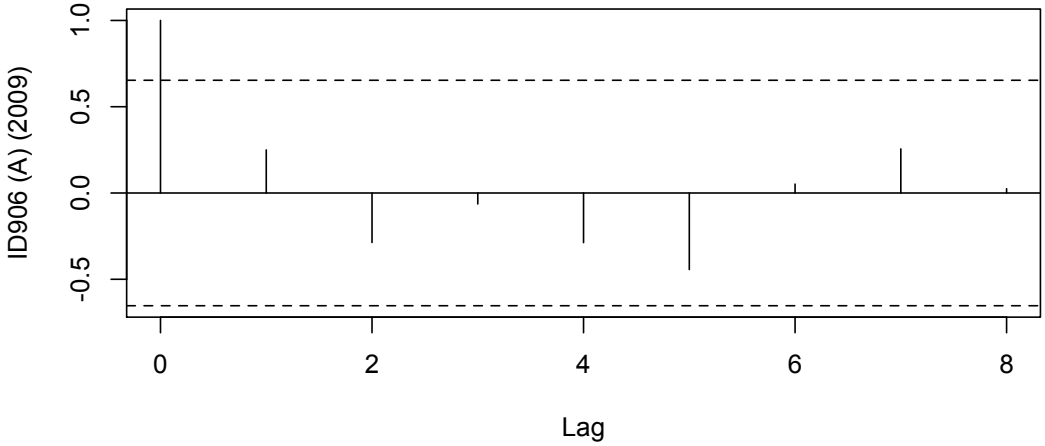
e)


ID904 (A) (2009)
1.0
0.5
0.0
-0.5
0
2
4
6
8
Lag

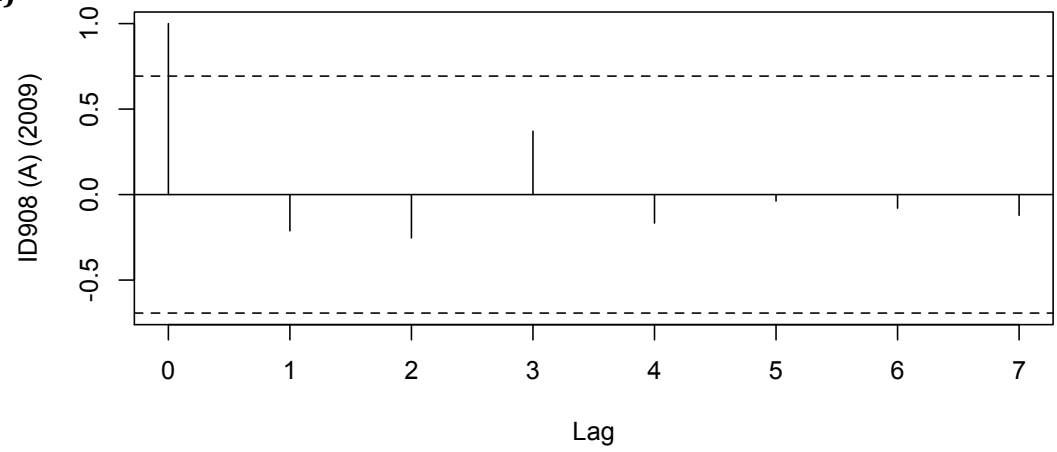
f)


ID905 (A) (2009)
1.0
0.5
0.0
-0.5
0
2
4
6
8
Lag

g)


ID906 (A) (2009)
1.0
0.5
0.0
-0.5
0
2
4
6
8
Lag

h)


ID908 (A) (2009)
1.0
0.5
0.0
-0.5
0
1
2
3
4
5
6
7
Lag

The following 5 pages show:

Tables A3.4 - A3.12: The collinearity analyses for the nine re-sighted individuals' datasets (2007 - 2009; 2007 & 2008; 2008 & 2009; 2007 & 2009). The analyses were done using the Spearman's rank correlation coefficient. The *p* value is shown above and the r value is shown below. Significant results are in bold. See Figure 3.12 for a summary of the consistently collinear covariates. The covariates are: the proportion of time the pup is active (ACT); the density of females within a 10 m buffer zone of the target female (DEN); the distance between a mother and her pup (PUP); the distance between a mother and her nearest pool (POOL); the mothers' location within her estimated home range (HOME); the amount of rainfall (RAIN); the air temperature (TEMP); the age of the pup (AGE); the nearest female neighbour (NFN). See Section 3.8 for more details on each of the covariates.

Table A3.4: The collinearity analyses for the 2007 data for the female's that were re-sighted in all three years (2007 - 2009; n = 8)

	ACT	DEN	PUP	POOL	HOME	RAIN	TEMP	AGE	NFN
ACT	-	0.303	0.083	0.881	0.701	0.533	0.834	0.121	0.201
	-	0.043	-0.072	-0.006	-0.016	-0.026	0.009	-0.065	-0.054
DEN		-	0.051	**<0.001**	**<0.001**	**0.012**	0.737	0.521	**<0.001**
		-	0.082	**-0.16**	**0.2**	**-0.105**	0.014	-0.027	**-0.489**
PUP			-	**<0.001**	**<0.001**	0.907	**0.014**	**<0.001**	0.67
			-	**-0.31**	**-0.251**	-0.005	**0.103**	**-0.209**	-0.018
POOL				-	0.673	0.219	**<0.001**	**0.013**	**0.01**
				-	0.018	0.051	**-0.197**	**0.104**	**0.108**
HOME					-	0.818	0.242	**<0.001**	**0.031**
					-	-0.01	-0.049	**0.217**	**-0.09**
RAIN						-	0.117	**<0.001**	0.085
						-	0.066	**0.168**	0.072
TEMP							-	0.414	0.297
							-	-0.034	-0.044
AGE								-	0.663
								-	-0.018
NFN									-
									-

Table A3.5: The collinearity analyses for the 2008 data for the female's that were re-sighted in all three years (2007 - 2009; n = 8)

	ACT	DEN	PUP	POOL	HOME	RAIN	TEMP	AGE	NFN
ACT	-	0.787	0.293	0.3	**<0.001**	0.518	**0.014**	**0.029**	0.368
	-	-0.009	-0.035	0.035	**-0.114**	-0.022	**0.082**	**-0.073**	0.03
DEN		-	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
		-	**0.165**	**-0.497**	**0.148**	**-0.142**	**0.2**	**0.219**	**-0.671**
PUP			-	**<0.001**	**<0.001**	**0.001**	**<0.001**	**<0.001**	**<0.001**
			-	**-0.474**	**-0.167**	**-0.109**	**0.118**	**-0.199**	**-0.132**
POOL				-	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
				-	**-0.136**	**0.186**	**-0.242**	**-0.111**	**0.313**
HOME					-	0.059	0.937	**<0.001**	0.063
					-	-0.063	-0.003	**0.119**	-0.063
RAIN						-	0.662	**<0.001**	**<0.001**
						-	0.0146	**0.116**	**0.149**
TEMP							-	**<0.001**	0.201
							-	**-0.302**	-0.043
AGE								-	**<0.001**
								-	**-0.177**
NFN									-
									-

Table A3.6: The collinearity analyses for the 2009 data for the female's that were re-sighted in all three years (2007 - 2009; n = 8)

	ACT	DEN	PUP	POOL	HOME	RAIN	TEMP	AGE	NFN
ACT	-	0.784	0.168	0.108	**0.004**	**0.033**	0.286	**0.012**	0.236
	-	-0.001	-0.049	0.058	**-0.102**	**0.076**	-0.038	**-0.09**	0.042
DEN		-	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.078	**<0.001**	**<0.001**
		-	**-0.187**	**-0.156**	**0.189**	**-0.6**	-0.063	**0.154**	**-0.727**
PUP			-	**<0.001**	0.435	0.87	**0.022**	0.762	**<0.001**
			-	**-0.264**	0.028	0.006	**-0.082**	-0.011	**0.128**
POOL				-	**<0.001**	**<0.001**	0.385	**<0.001**	0.166
				-	**-0.436**	**0.178**	-0.031	**-0.278**	0.05
HOME					-	**<0.001**	**<0.001**	**<0.001**	**<0.001**
					-	**-0.159**	**0.134**	**0.329**	**-0.151**
RAIN						-	**<0.001**	**<0.001**	**0.003**
						-	**0.171**	**-0.184**	**0.106**
TEMP							-	**<0.001**	0.917
							-	**0.264**	-0.004
AGE								-	**0.002**
								-	**-0.108**
NFN									-
									-

Table A3.7: The collinearity analyses for the 2007 data for the female's that were re-sighted in 2007 & 2008 (n = 9)

	ACT	DEN	PUP	POOL	HOME	RAIN	TEMP	AGE	NFN
ACT	-	0.111	0.074	0.92	0.557	0.633	0.755	**0.034**	0.163
	-	0.0627	-0.07	0.004	-0.023	-0.019	0.012	**-0.083**	-0.055
DEN		-	0.061	**<0.001**	**<0.001**	**0.009**	0.105	0.106	**<0.001**
		-	0.074	**-0.147**	**0.145**	**-0.103**	0.064	-0.063	**-0.476**
PUP			-	**<0.001**	**<0.001**	0.292	**0.019**	**<0.001**	0.46
			-	**-0.313**	**-0.231**	-0.041	**0.092**	**-0.22**	-0.029
POOL				-	0.659	**0.018**	**<0.001**	**0.028**	**<0.001**
				-	0.017	**0.093**	**-0.185**	**0.086**	**0.143**
HOME					-	0.813	0.143	**<0.001**	0.054
					-	-0.009	-0.058	**0.184**	-0.076
RAIN						-	0.178	**<0.001**	**0.014**
						-	0.053	**0.187**	**0.096**
TEMP							-	0.279	**0.039**
							-	-0.043	**-0.081**
AGE								-	0.892
								-	0.005
NFN									-
									-

Table A3.8: The collinearity analyses for the 2008 data for the female's that were re-sighted in 2007 & 2008 (n = 9)

	ACT	DEN	PUP	POOL	HOME	RAIN	TEMP	AGE	NFN
ACT	- -	0.945 0.002	0.231 -0.038	0.137 0.048	**<0.003** **-0.095**	0.23 -0.038	**0.039** **0.066**	0.044 -0.065	0.536 0.02
DEN		- -	**<0.001** **0.113**	**<0.001** **-0.434**	**<0.001** **0.188**	**<0.001** **-0.147**	**<0.001** **0.194**	**<0.001** **0.254**	**<0.001** **-0.666**
PUP			- -	**<0.001** **-0.466**	**<0.001** **-0.21**	**<0.001** **-0.116**	**<0.001** **0.112**	**<0.001** **-0.229**	**<0.001** **-0.118**
POOL				- -	**0.007** **-0.087**	**<0.001** **0.16**	**<0.001** **-0.228**	**0.018** **-0.076**	**<0.001** **0.295**
HOME					- -	**0.029** **-0.07**	1 0.0001	**<0.001** **0.18**	**0.016** **-0.077**
RAIN						- -	0.574 0.018	**<0.001** **0.13**	**<0.001** **0.161**
TEMP							- -	**<0.001** **-0.288**	0.179 -0.043
AGE								- -	**<0.001** **-0.19**
NFN									- -

Table A3.9: The collinearity analyses for the 2008 data for the female's that were re-sighted in 2008 & 2009 (n = 15)

	ACT	DEN	PUP	POOL	HOME	RAIN	TEMP	AGE	NFN
ACT	- -	0.434 -0.019	0.572 -0.014	0.226 0.03	**<0.001** **-0.098**	0.372 -0.022	**0.007** **0.066**	0.078 -0.043	0.133 0.037
DEN		- -	0.221 0.03	**<0.001** **-0.458**	**<0.001** **0.219**	**0.002** **-0.075**	**<0.001** **0.184**	**<0.001** **0.139**	**<0.001** **-0.589**
PUP			- -	**<0.001** **-0.35**	**<0.001** **-0.27**	**0.012** **-0.062**	**0.001** **0.08**	**<0.001** **-0.172**	**0.021** **-0.057**
POOL				- -	**0.009** **-0.064**	**<0.001** **0.142**	**<0.001** **-0.222**	0.389 -0.021	**<0.001** **0.287**
HOME					- -	0.102 -0.04	0.179 -0.033	**<0.001** **0.196**	**<0.001** **-0.128**
RAIN						- -	**0.009** **0.064**	**0.002** **0.076**	**<0.001** **0.082**
TEMP							- -	**<0.001** **-0.305**	0.085 -0.042
AGE								- -	**<0.001** **-0.153**
NFN									- -

Table A3.10: The collinearity analyses for the 2009 data for the female's that were re-sighted in 2008 & 2009 (n = 15)

	ACT	DEN	PUP	POOL	HOME	RAIN	TEMP	AGE	NFN
ACT	-	**0.025**	**0.039**	0.353	**0.001**	0.07	0.504	**0.002**	**<0.001**
	-	**-0.058**	**-0.053**	0.024	**-0.083**	0.047	-0.017	**-0.082**	**0.087**
DEN		-	**<0.001**	**0.014**	**<0.001**	**<0.001**	0.332	**0.005**	**<0.001**
		-	**-0.129**	**-0.064**	**0.23**	**-0.184**	0.025	**0.073**	**-0.74**
PUP			-	**<0.001**	**0.001**	0.052	**0.001**	**0.005**	0.109
			-	**-0.17**	**-0.084**	0.05	**-0.084**	**-0.073**	0.041
POOL				-	**<0.001**	**<0.001**	**0.009**	**<0.001**	0.537
				-	**-0.326**	**0.093**	**0.068**	**-0.089**	0.016
HOME					-	**<0.001**	**<0.001**	**<0.001**	**<0.001**
					-	**-0.235**	**0.099**	**0.29**	**-0.156**
RAIN						-	**<0.001**	**<0.001**	**<0.001**
						-	**0.104**	**-0.247**	**0.129**
TEMP							-	**<0.001**	0.43
							-	**0.166**	-0.02
AGE								-	0.213
								-	-0.032
NFN									-
									-

Table A3.11: The collinearity analyses for the 2007 data for the female's that were re-sighted in 2007 & 2009 (n = 9)

	ACT	DEN	PUP	POOL	HOME	RAIN	TEMP	AGE	NFN
ACT	-	0.271	**0.016**	0.968	0.656	0.869	0.789	0.121	0.26
	-	0.044	**-0.096**	-0.002	-0.018	-0.007	0.011	-0.062	-0.045
DEN		-	**0.03**	**<0.001**	**<0.001**	**0.001**	0.559	0.333	**<0.001**
		-	**0.087**	**-0.182**	**0.195**	**-0.126**	0.023	-0.039	**-0.478**
PUP			-	**<0.001**	**<0.001**	0.801	**0.004**	**<0.001**	0.389
			-	**-0.331**	**-0.184**	-0.01	**0.114**	**-0.219**	-0.034
POOL				-	0.404	0.055	**<0.001**	**0.002**	**<0.001**
				-	-0.033	0.077	**-0.187**	**0.122**	**0.133**
HOME					-	0.886	0.285	**<0.001**	**0.01**
					-	0.006	-0.043	**0.204**	**-0.103**
RAIN						-	0.146	**<0.001**	0.11
						-	0.058	**0.184**	0.064
TEMP							-	0.1	0.159
							-	-0.066	-0.056
AGE								-	0.954
								-	-0.002
NFN									-
									-

Table A3.12: The collinearity analyses for the 2009 data for the female's that were re-sighted in 2007 & 2009 (n = 9)

	ACT	DEN	PUP	POOL	HOME	RAIN	TEMP	AGE	NFN
ACT	-	0.465	0.436	0.054	**0.001**	**0.039**	0.386	**0.005**	0.132
	-	-0.025	-0.026	0.065	**-0.109**	**0.07**	-0.029	**-0.094**	0.051
DEN		-	**0.002**	**<0.001**	**<0.001**	**<0.001**	0.11	**<0.001**	**<0.001**
		-	**-0.105**	**-0.201**	**0.19**	**-0.141**	-0.054	**0.134**	**-0.731**
PUP			-	**<0.001**	0.727	0.857	**0.006**	0.161	**0.034**
			-	**-0.272**	-0.012	-0.006	**-0.092**	-0.047	**0.071**
POOL				-	**<0.001**	**<0.001**	**0.03**	**<0.001**	**0.001**
				-	**-0.446**	**0.134**	**-0.073**	**-0.291**	**0.107**
HOME					-	**0.001**	**<0.001**	**<0.001**	**<0.001**
					-	**-0.109**	**0.162**	**0.38**	**-0.16**
RAIN						-	**<0.001**	**<0.001**	**0.012**
						-	**0.166**	**-0.124**	**0.085**
TEMP							-	**<0.001**	0.394
							-	**0.283**	-0.029
AGE								-	**0.002**
								-	**-0.102**
NFN									-
									-

Chapter 4: Appendix

Table A4.1: The results of the Kruskal-Wallis tests and the *post hoc* multiple comparison tests for the proportion of time spent in each behavioural category between the three lactation periods (LP) for all re-sighted females for each of the three breeding seasons. Significant results are in bold. The *post hoc* analyses show the observed (Obs.) and critical (Crit.) values (d.f. = 2). The full name of each of the behavioural categories is shown in the footnote. The number of individuals included in lactation periods 1, 2 and 3 for 2007 (11, 11, 9), 2008 (16, 17, 15) and 2009 (15, 15, 14).

				LP1 - LP2		LP1 - LP3		LP2 - LP3	
Year	BEH	Chi-Sq	*p*	Obs.	Crit.	Obs.	Crit.	Obs.	Crit.
2007	R	2.872	0.238	5.636	9.281	0.313	9.783	5.950	9.783
	CM	2.193	0.334	3.591	9.281	2.354	9.783	5.944	9.783
	PC	1.475	0.478	2.773	9.281	2.136	9.783	4.909	9.783
	A	3.417	0.181	2.818	9.281	4.697	9.783	7.515	9.783
	L	4.267	0.118	1.091	9.281	7.747	9.783	6.657	9.783
	MP	2.435	0.296	6.000	9.281	2.374	9.783	3.626	9.783
	PINT	5.496	0.064	8.136	9.281	1.328	9.783	6.808	9.783
	AGG	4.951	0.084	6.182	9.281	1.449	9.783	7.631	9.783
2008	R	5.418	0.067	1.676	11.674	10.900	12.045	9.224	11.873
	CM	2.076	0.354	0.634	11.674	6.581	12.045	5.947	11.873
	PC	**10.545**	**0.005**	1.388	11.674	**14.727**	**12.045**	13.339	11.873
	A	1.831	0.400	6.108	11.674	5.377	12.045	0.731	11.873
	L	**11.751**	**0.003**	0.976	11.674	**15.194**	**12.045**	**14.218**	**11.873**
	MP	**7.256**	**0.027**	7.403	11.674	**13.510**	**12.045**	6.108	11.873
	PINT	**6.721**	**0.035**	**12.592**	**11.674**	6.729	12.045	5.863	11.873
	AGG	2.218	0.330	7.182	11.674	3.360	12.045	3.822	11.873
2009	R	2.962	0.227	6.967	11.229	7.098	11.428	0.131	11.428
	CM	0.549	0.760	2.367	11.229	1.069	11.428	3.436	11.428
	PC	0.420	0.811	2.900	11.229	0.664	11.428	2.236	11.428
	A	1.512	0.470	3.467	11.229	2.353	11.428	5.819	11.428
	L	1.945	0.378	0.233	11.229	5.826	11.428	5.593	11.428
	MP	**12.614**	**0.002**	8.433	11.229	**16.945**	**11.428**	8.512	11.428
	PINT	**14.479**	**<0.001**	**17.667**	**11.229**	7.786	11.428	9.881	11.428
	AGG	2.837	0.242	7.000	11.229	6.224	11.428	0.776	11.428

R = Resting; CM = Comfort Movement; PC = Pup Check; A = Alert; L = Locomotion; MP = Presenting & Nursing; PINT = Pup Interactions; AGG = Aggression

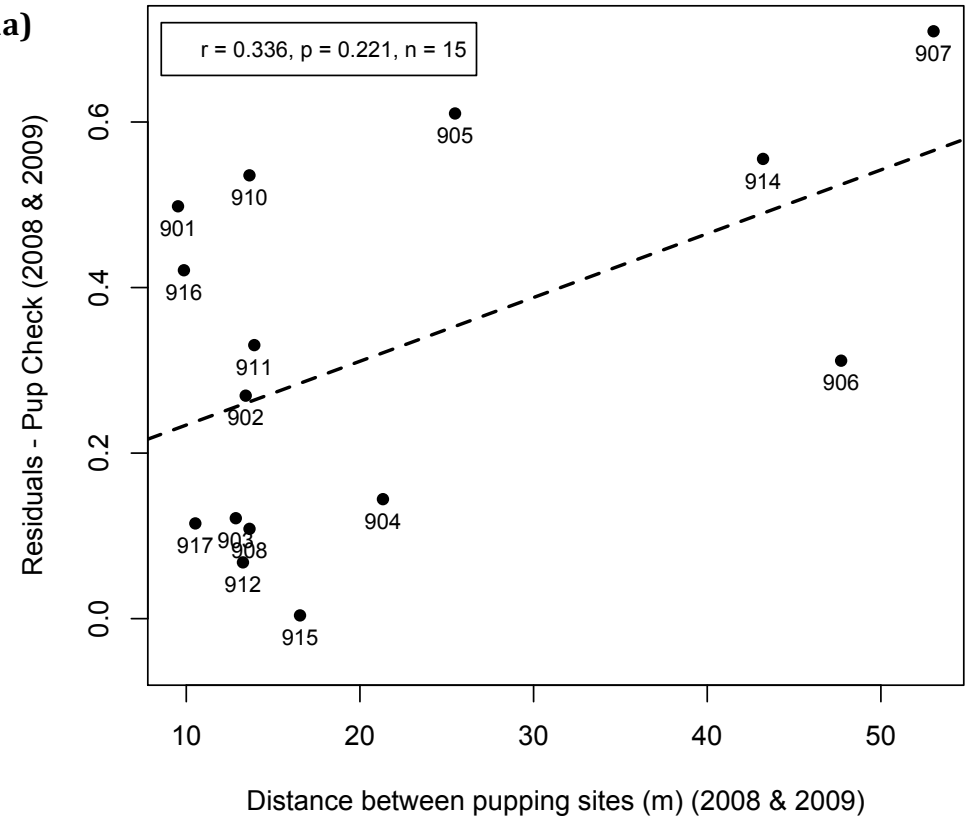
Table A4.2: ICC3 analyses for all 3 years (n = 8), 2007 & 2008 (n = 9), 2008 & 2009 (n = 16), 2007 & 2009 (n = 9), the Lactation Period(s) (LP) used are based on the lactation period analyses (Table A4.1). All significant results are in bold. Where ICC values are negative the best estimate for repeatability is zero (Hayes & Jenkins, 1997; Bell et al., 2009). The lower and upper columns show the 95% confidence limits.

Behaviour	Years	LP	ICC	F	*p*	lower	upper
Resting	2007-2009	ALL	0.16	1.6	0.22	-0.22	0.67
	2007 & 2008	ALL	0.43	2.5	0.11	-0.28	0.83
	2008 & 2009	ALL	0.37	2.2	0.078	-0.15	0.73
	2007 & 2009	ALL	0.28	1.8	0.22	-0.43	0.77
Comfort Movement	2007-2009	ALL	-0.097	0.73	0.65	-0.35	0.44
	2007 & 2008	ALL	0.02	1.04	0.48	-0.62	0.64
	2008 & 2009	ALL	-0.22	0.96	0.53	-0.51	0.48
	2007 & 2009	ALL	-0.077	0.86	0.58	-0.68	0.58
Pup Check	2007-2009	MID	0.24	1.9	0.14	-0.17	0.72
	2007 & 2008	MID	0.31	1.9	0.19	-0.40	0.79
	2008 & 2009	**MID**	**0.75**	**7**	**<0.001**	**0.41**	**0.91**
	2007 & 2009	MID	0.12	1.3	0.37	-0.55	0.7
Alert	**2007-2009**	**ALL**	**0.75**	**10.2**	**<0.001**	**0.40**	**0.94**
	2007 & 2008	**ALL**	**0.72**	**6**	**0.01**	**0.15**	**0.93**
	2008 & 2009	**ALL**	**0.65**	**4.7**	**0.003**	**0.23**	**0.87**
	2007 & 2009	**ALL**	**0.80**	**8.8**	**0.003**	**0.33**	**0.95**
Locomotion	2007-2009	MID	0.32	2.4	0.078	-0.108	0.77
	2007 & 2008	MID	0.23	1.6	0.26	-0.47	0.75
	2008 & 2009	MID	0.28	1.8	0.15	-0.25	0.68
	2007 & 2009	MID	0.47	2.8	0.084	-0.23	0.85
Presenting & Nursing	**2007-2009**	**MID**	**0.51**	**4.1**	**0.012**	**0.063**	**0.85**
	2007 & 2008	MID	0.33	2	0.18	-0.38	0.8
	2008 & 2009	**MID**	**0.52**	**3.2**	**0.02**	**0.028**	**0.81**
	2007 & 2009	MID	0.30	1.9	0.20	-0.41	0.79
Pup Interactions	2007-2009	MID	0.15	1.5	0.24	-0.23	0.66
	2007 & 2008	MID	0.2	1.5	0.29	-0.5	0.74
	2008 & 2009	**MID**	**0.58**	**3.7**	**0.01**	**0.11**	**0.83**
	2007 & 2009	**MID**	**0.64**	**4.5**	**0.024**	**0.007**	**0.93**
Aggression	**2007-2009**	**ALL**	**0.57**	**5.0**	**0.005**	**0.136**	**0.88**
	2007 & 2008	**ALL**	**0.64**	**4.5**	**0.024**	**0.006**	**0.9**
	2008 & 2009	**ALL**	**0.57**	**3.6**	**0.011**	**0.097**	**0.83**
	2007 & 2009	ALL	0.13	1.3	0.36	-0.55	0.71

The following 9 pages show:

Figures A4.1 - A4.9: the partial regression plots for the distance between the **a)** pupping site (m) and the **b)** centre of the core area of the home range (m) between the breeding seasons, plotted against the absolute residuals of the repeatability estimates for: **A4.1)**. Pup check (2007 & 2008) **A4.2, A4.3, A4.4)**. Alert (2007 & 2008; 2008 & 2009; 2007 & 2009, respectively) **A4.5)**. Presenting & nursing (2008 & 2009) **A4.6, A4.7)**. Pup interactions (2008 & 2009; 2007 & 2009, respectively) **A4.8, A4.9).** Aggression (2007 & 2008; 2008 & 2009, respectively). The results of the Spearman's rank correlation coefficient are shown in the legend within each of the plots. The dashed black line represents the line-of-best fit.

A4.1a)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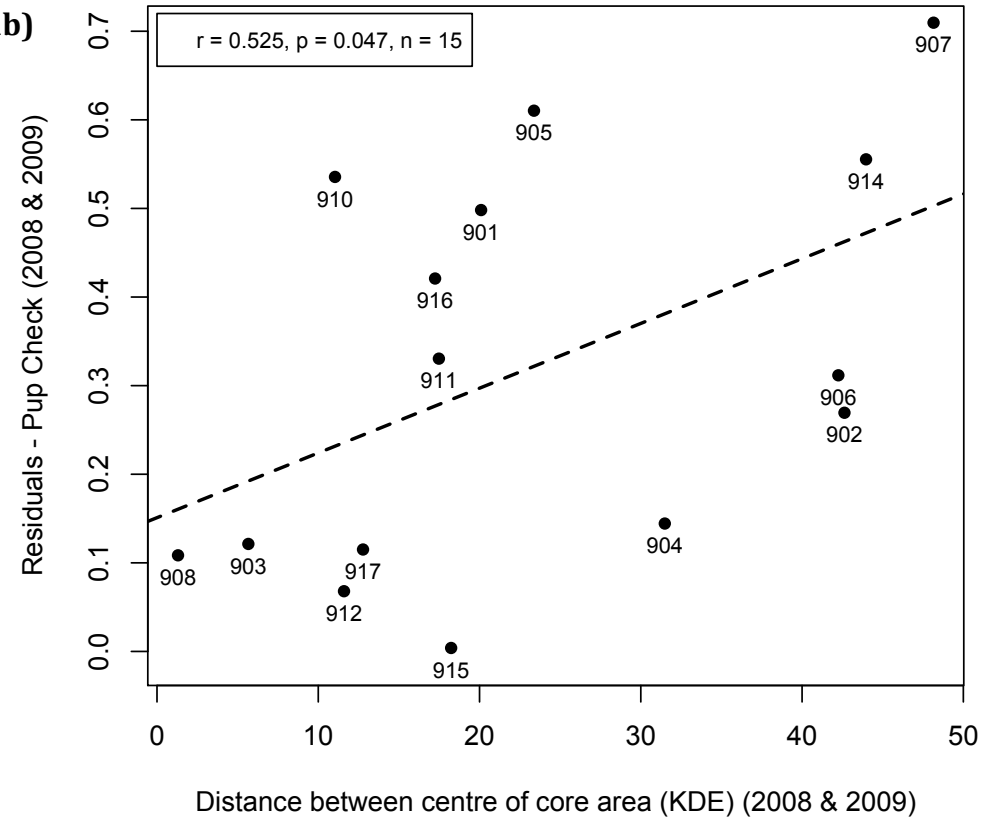
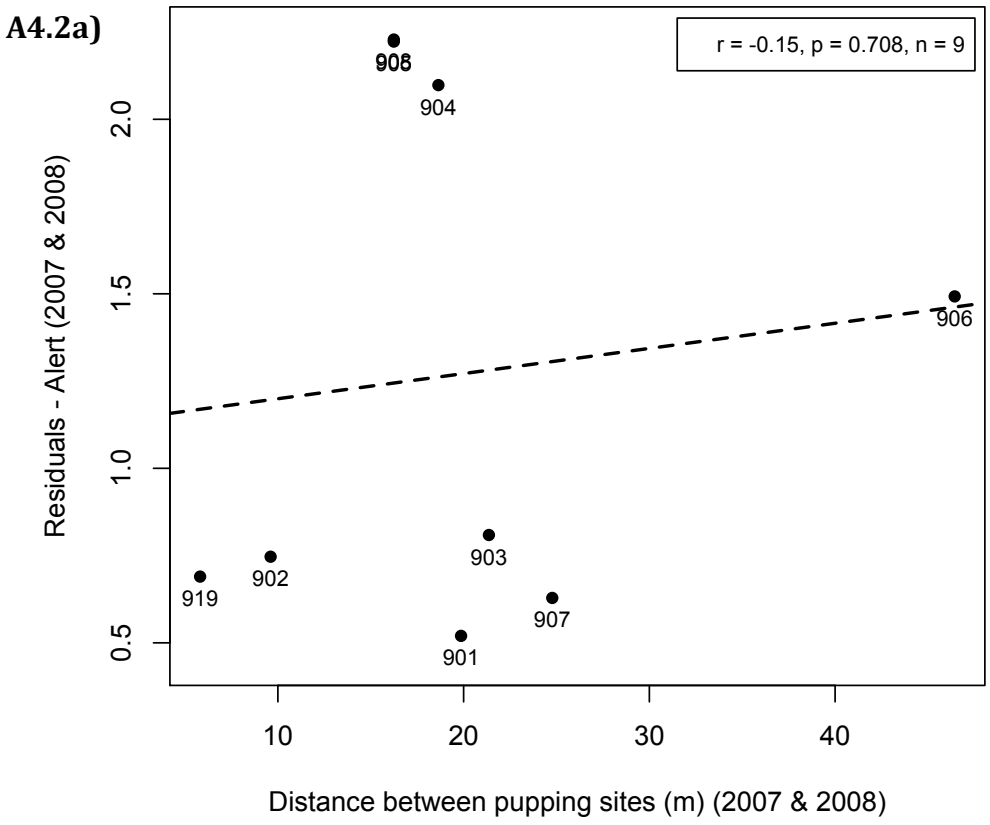
Residuals - Pup Check (2008 & 2009)
Distance between pupping sites (m) (2008 & 2009)
907
905
914
910
901
916
911
906
902
904
917
903
908
912
915

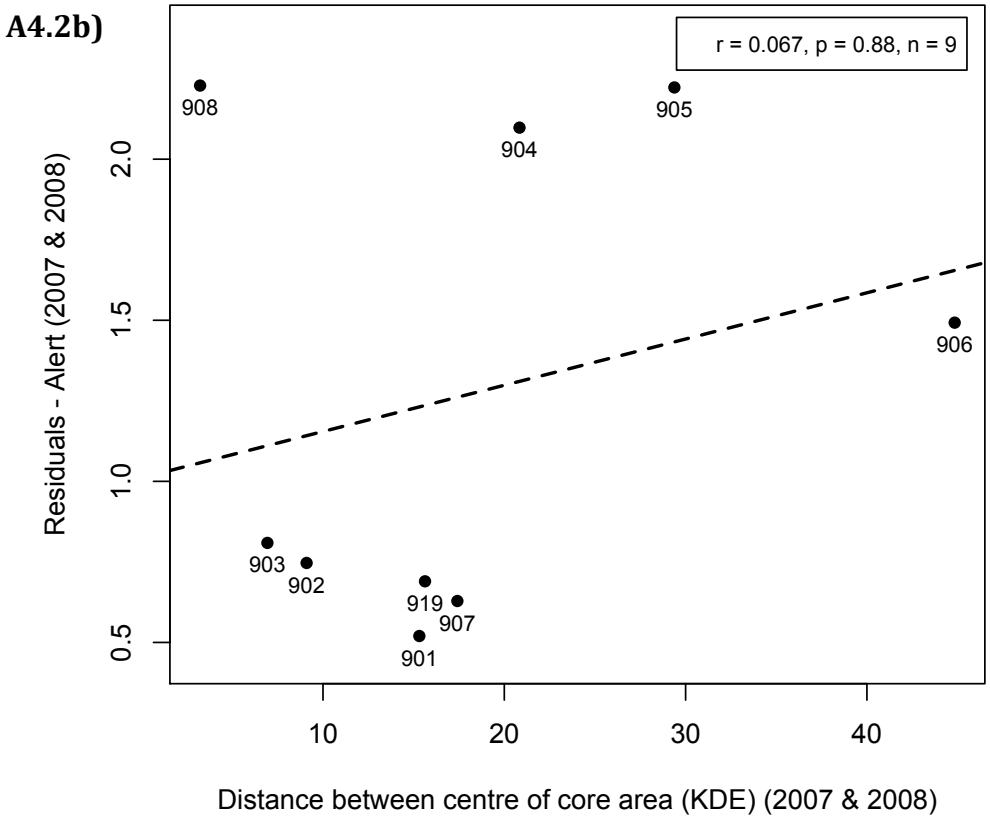
A4.1b)


r = 0.525, p = 0.047, n = 15
Residuals - Pup Check (2008 & 2009)
Distance between centre of core area (KDE) (2008 & 2009)
907
905
914
910
901
916
911
906
902
904
908
903
917
912
915

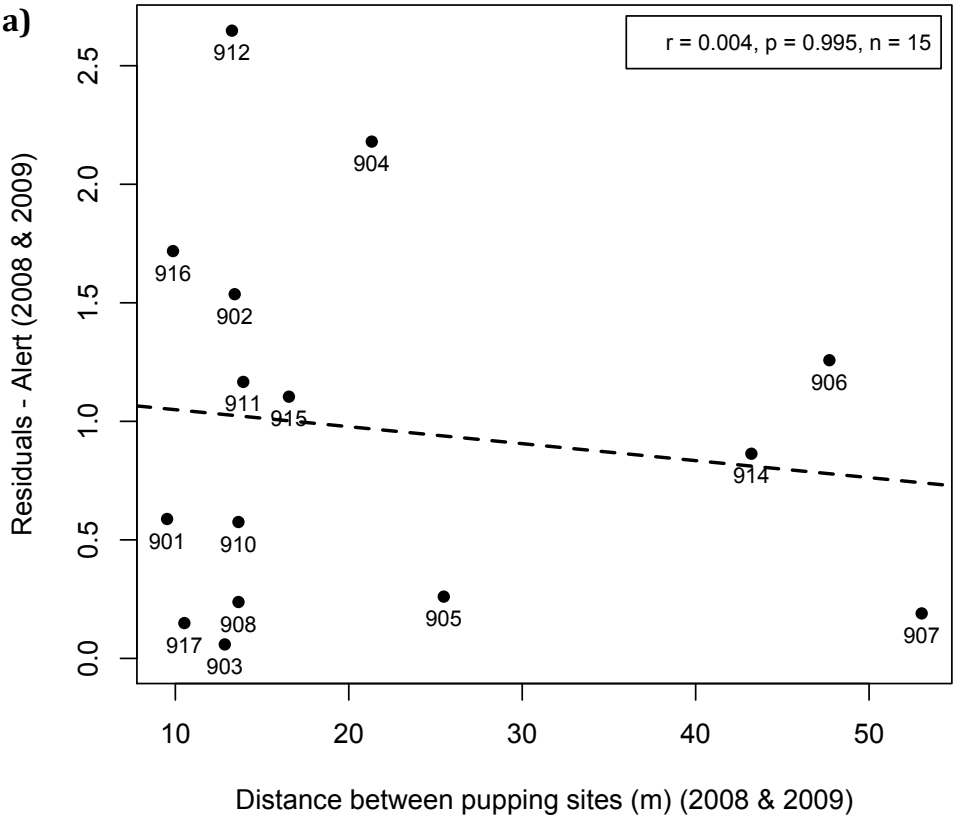
A4.2a)


r = -0.15, p = 0.708, n = 9
Residuals - Alert (2007 & 2008)
Distance between pupping sites (m) (2007 & 2008)
908
904
906
903
902
919
907
901
0.5
1.0
1.5
2.0
10
20
30
40

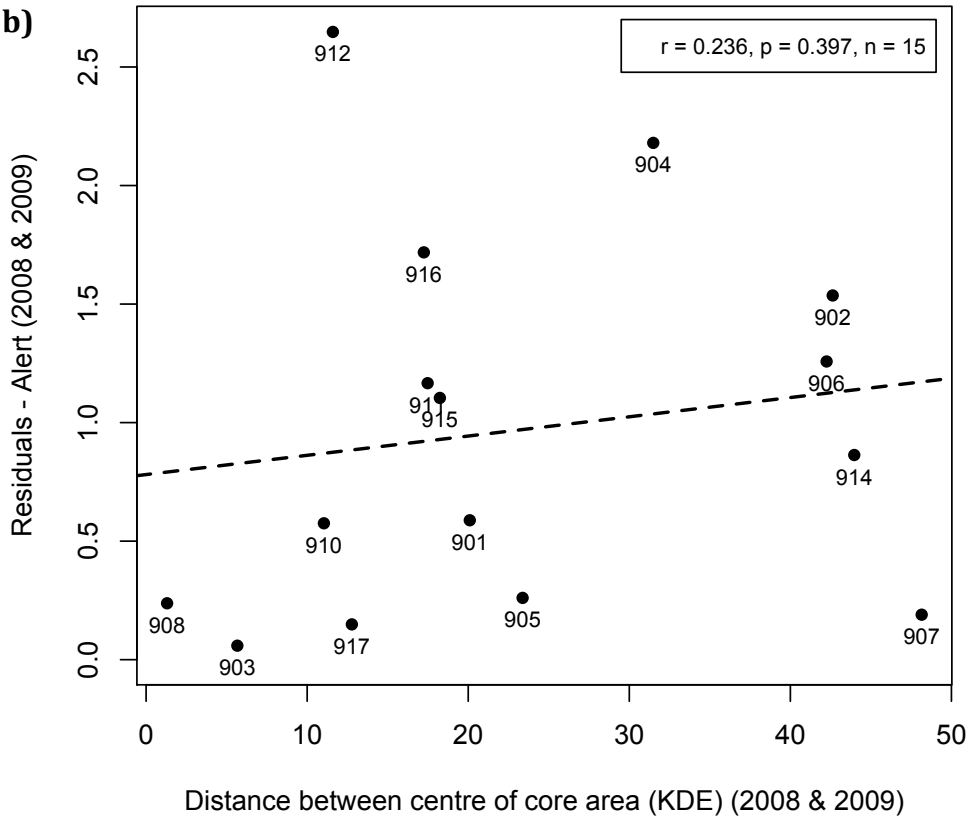
A4.2b)


r = 0.067, p = 0.88, n = 9
Residuals - Alert (2007 & 2008)
Distance between centre of core area (KDE) (2007 & 2008)
908
905
904
906
903
902
919
907
901
0.5
1.0
1.5
2.0
10
20
30
40

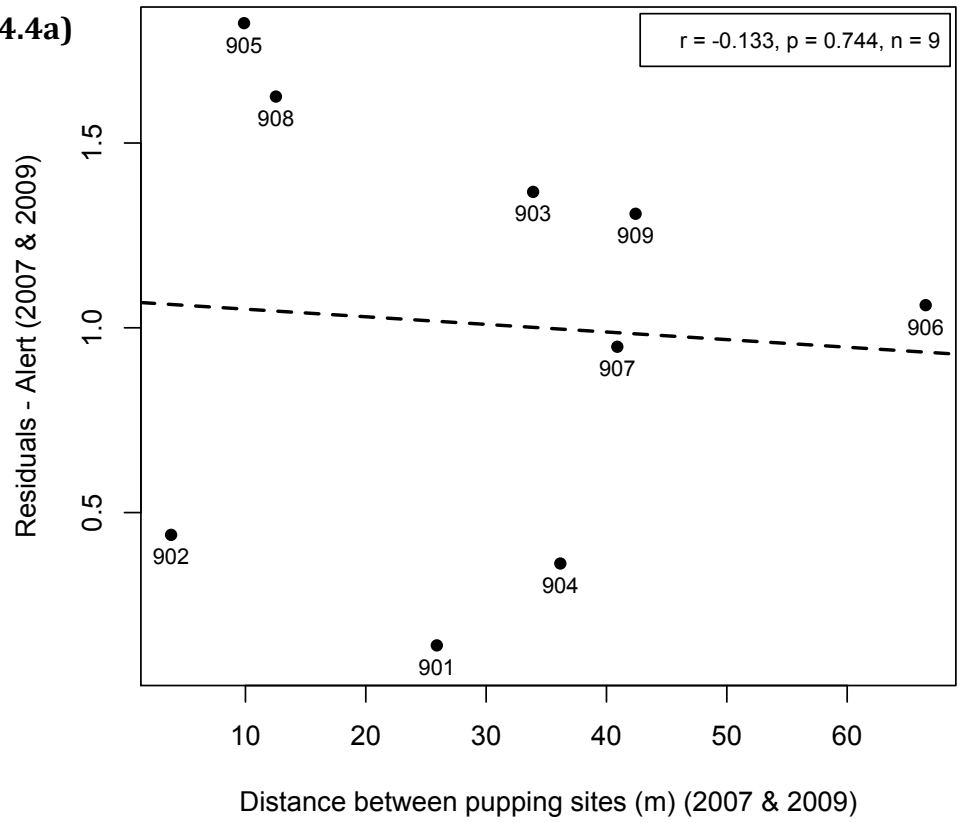
A4.3a)


r = 0.004, p = 0.995, n = 15
Residuals - Alert (2008 & 2009)
Distance between pupping sites (m) (2008 & 2009)
912
904
916
902
906
911
915
914
901
910
908
905
907
917
903
0.0
0.5
1.0
1.5
2.0
2.5
10
20
30
40
50

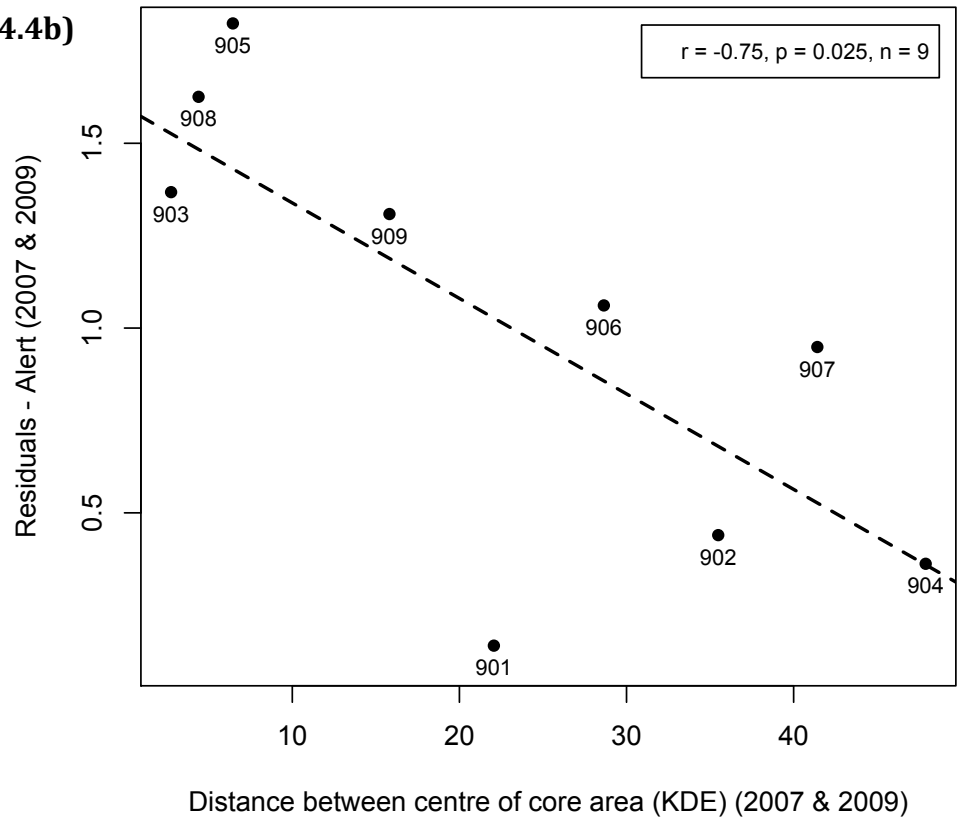
A4.3b)


r = 0.236, p = 0.397, n = 15
Residuals - Alert (2008 & 2009)
Distance between centre of core area (KDE) (2008 & 2009)
912
904
916
902
906
911
915
914
910
901
908
905
907
917
903
0.0
0.5
1.0
1.5
2.0
2.5
0
10
20
30
40
50

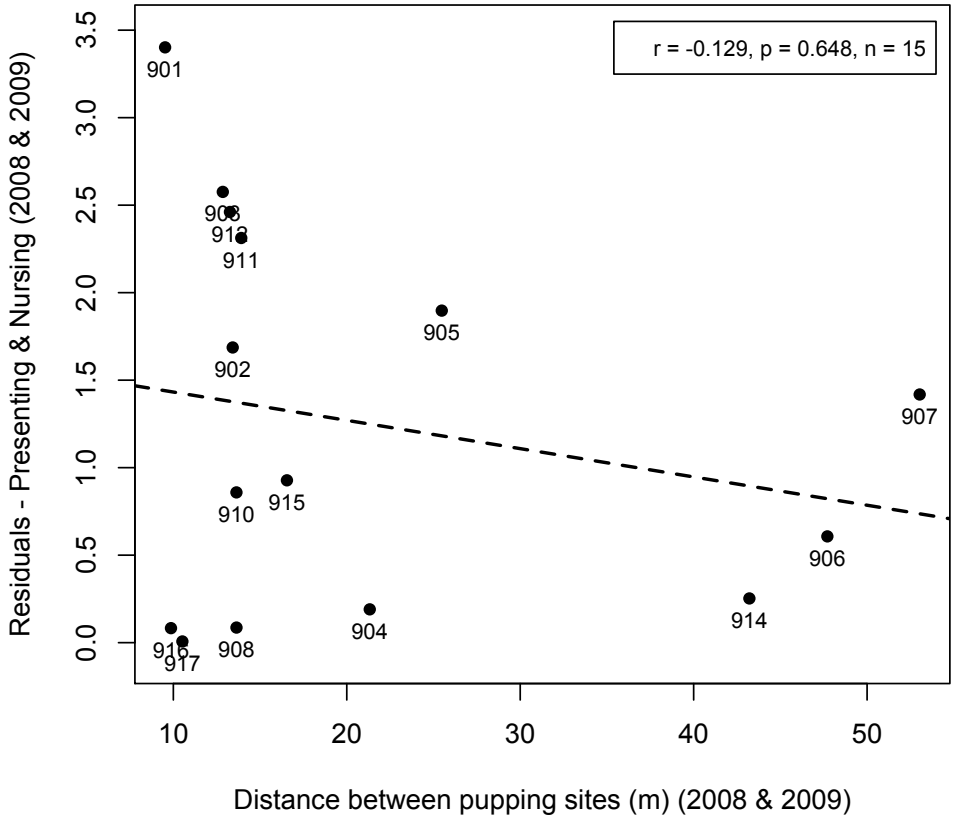
A4.4a)


r = -0.133, p = 0.744, n = 9
905
908
903
909
906
907
902
904
901
Residuals - Alert (2007 & 2009)
0.5
1.0
1.5
10
20
30
40
50
60
Distance between pupping sites (m) (2007 & 2009)

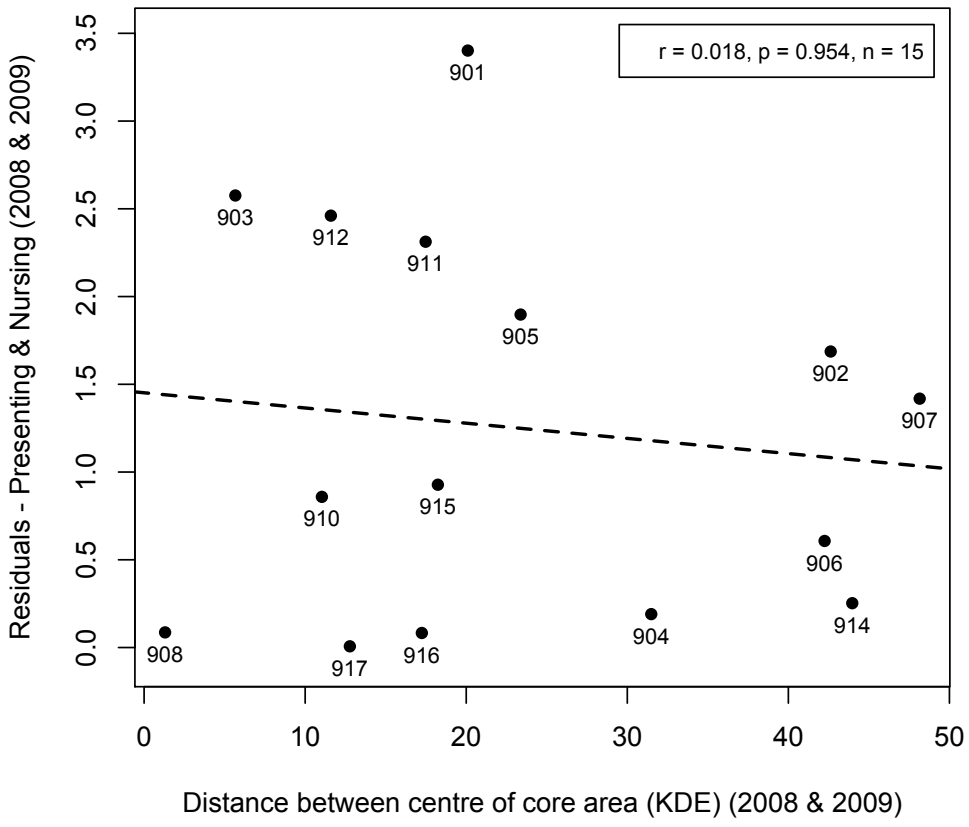
A4.4b)


r = -0.75, p = 0.025, n = 9
905
908
903
909
906
907
902
904
901
Residuals - Alert (2007 & 2009)
0.5
1.0
1.5
10
20
30
40
Distance between centre of core area (KDE) (2007 & 2009)

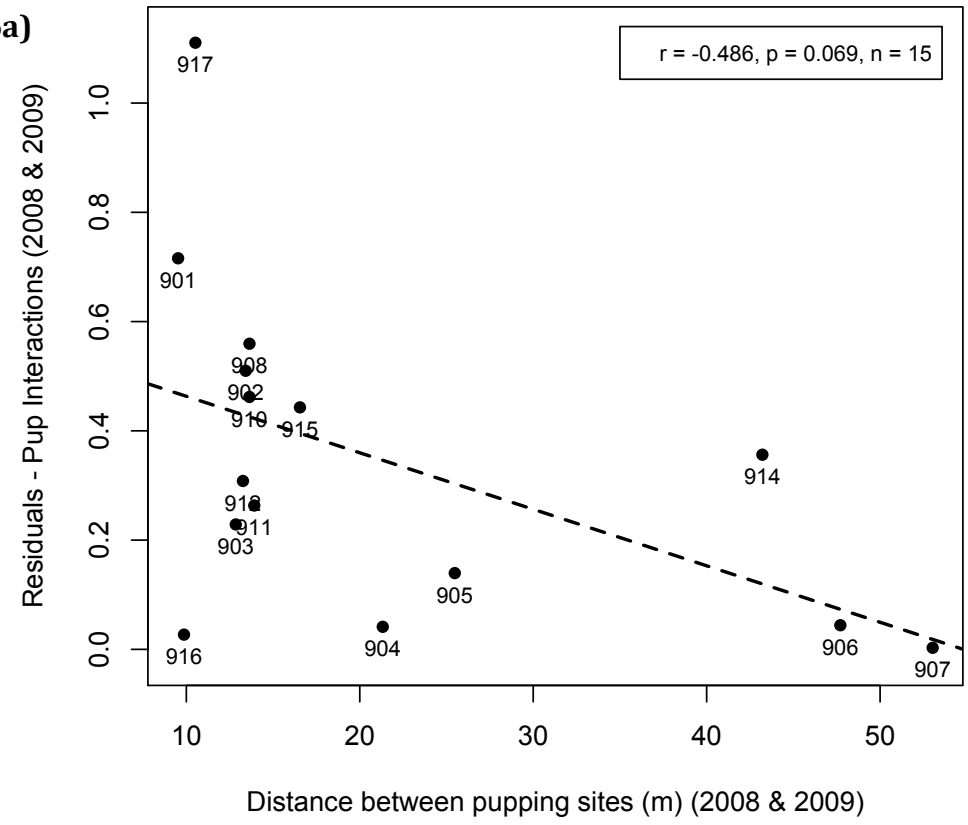
A4.5a)


r = -0.129, p = 0.648, n = 15
Residuals - Presenting & Nursing (2008 & 2009)
Distance between pupping sites (m) (2008 & 2009)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
10
20
30
40
50
901
903
913
911
905
902
907
915
910
906
914
904
916
917
908

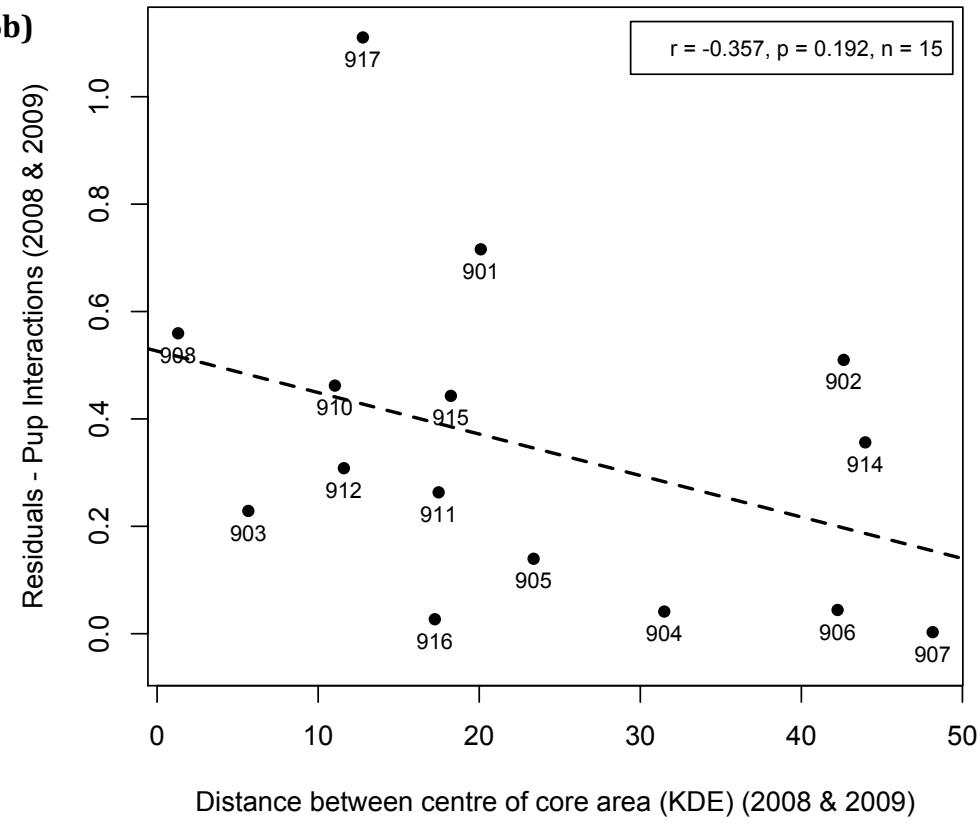
A4.5b)


r = 0.018, p = 0.954, n = 15
Residuals - Presenting & Nursing (2008 & 2009)
Distance between centre of core area (KDE) (2008 & 2009)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0
10
20
30
40
50
901
903
912
911
905
902
907
910
915
906
914
904
908
917
916

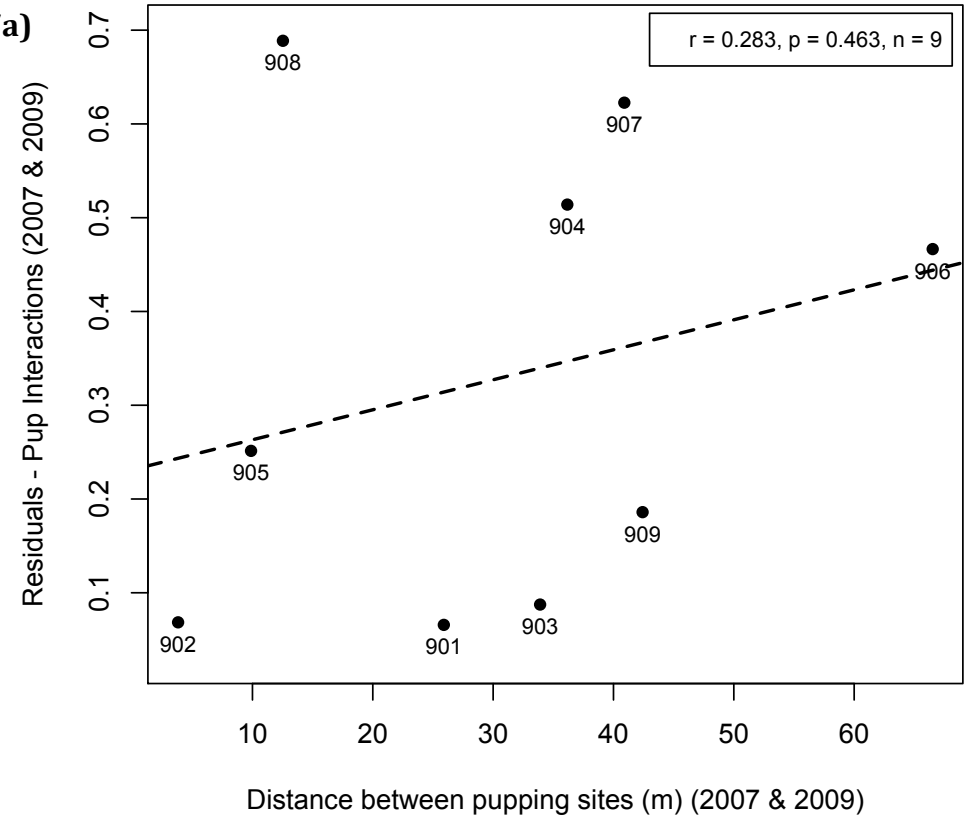
A4.6a)


r = -0.486, p = 0.069, n = 15
Residuals - Pup Interactions (2008 & 2009)
Distance between pupping sites (m) (2008 & 2009)
0.0
0.2
0.4
0.6
0.8
1.0
10
20
30
40
50
917
901
908
902
910
915
914
918
911
903
905
916
904
906
907

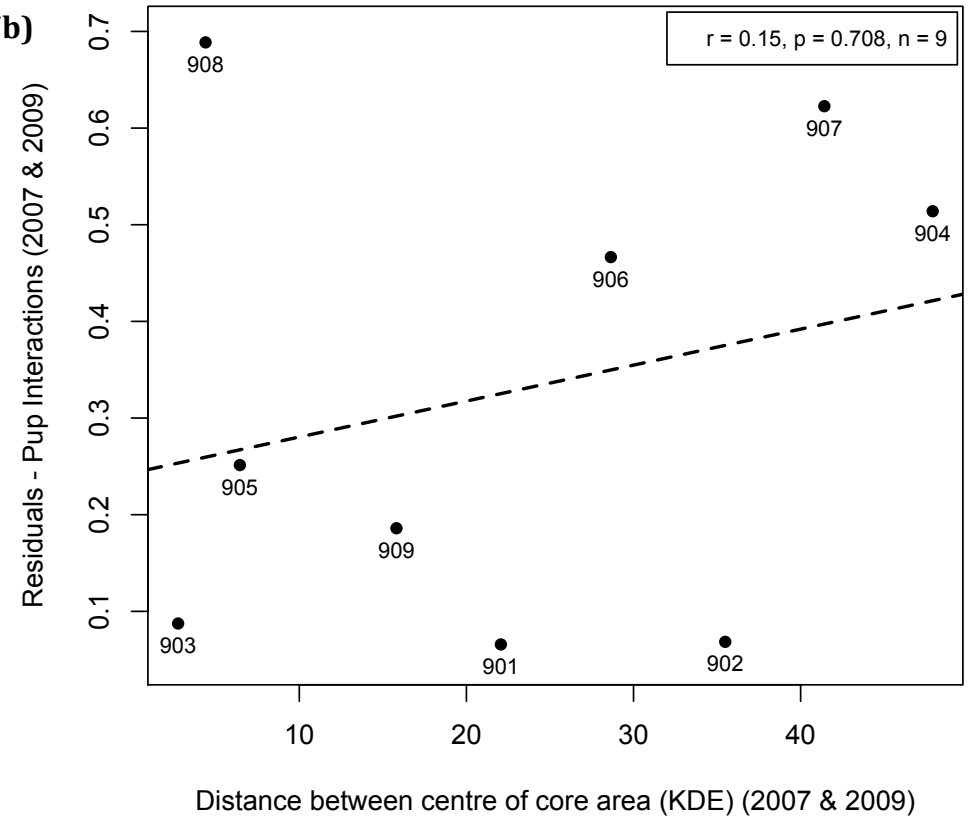
A4.6b)


r = -0.357, p = 0.192, n = 15
Residuals - Pup Interactions (2008 & 2009)
Distance between centre of core area (KDE) (2008 & 2009)
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
917
901
908
902
910
915
914
912
911
903
905
916
904
906
907

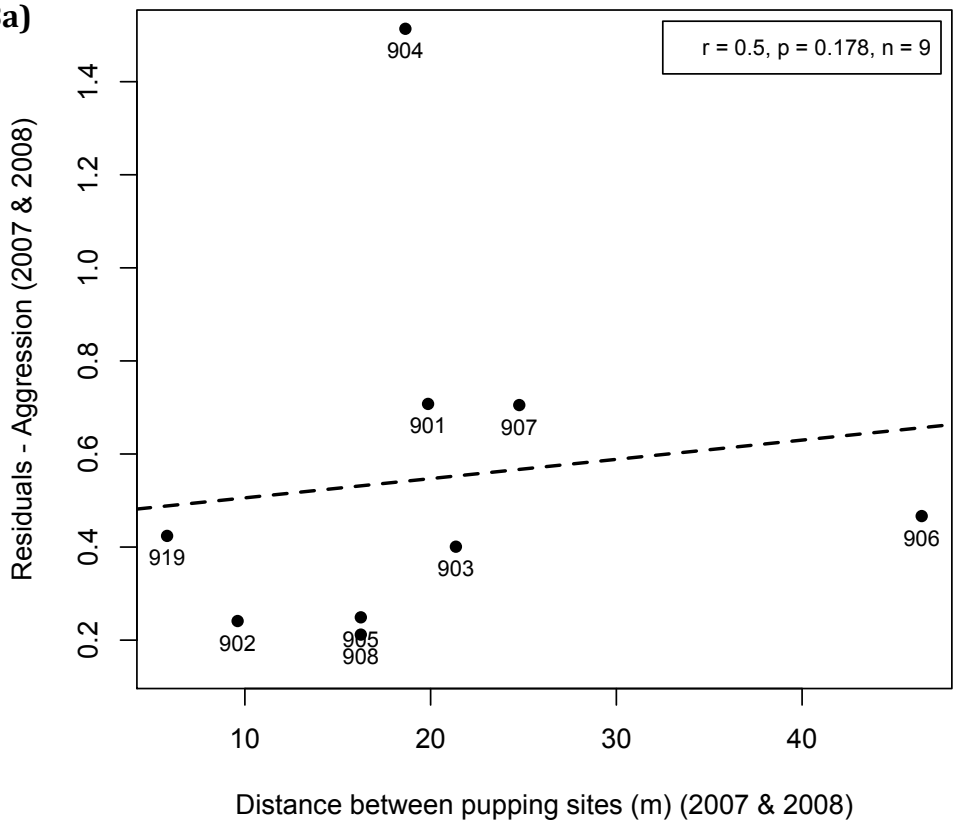
A4.7a)


r = 0.283, p = 0.463, n = 9
908
907
904
906
905
909
902
901
903
Residuals - Pup Interactions (2007 & 2009)
0.1
0.2
0.3
0.4
0.5
0.6
0.7
10
20
30
40
50
60
Distance between pupping sites (m) (2007 & 2009)

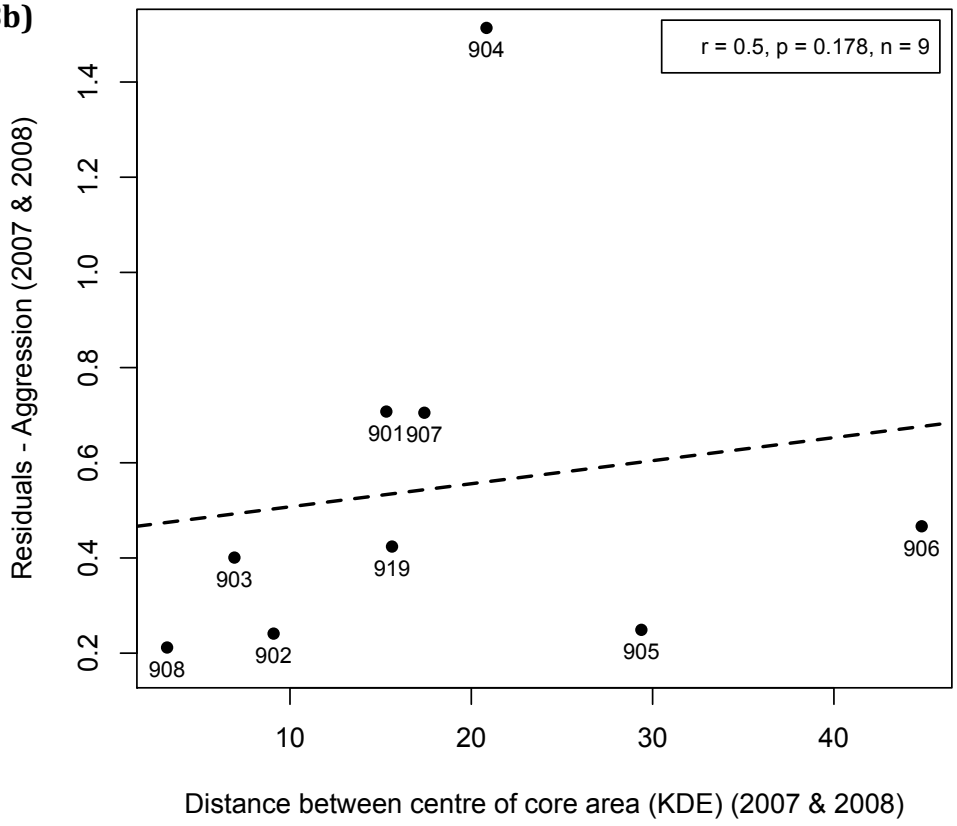
A4.7b)


r = 0.15, p = 0.708, n = 9
908
907
904
906
905
909
903
901
902
Residuals - Pup Interactions (2007 & 2009)
0.1
0.2
0.3
0.4
0.5
0.6
0.7
10
20
30
40
Distance between centre of core area (KDE) (2007 & 2009)

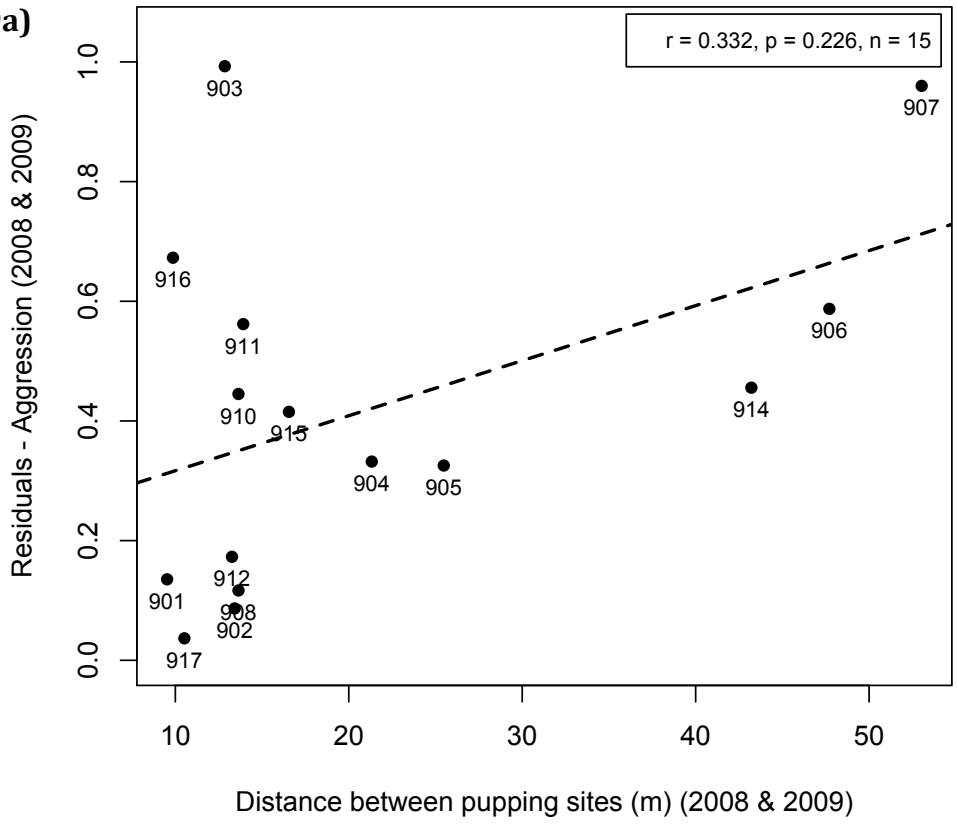
A4.8a)


r = 0.5, p = 0.178, n = 9
Residuals - Aggression (2007 & 2008)
Distance between pupping sites (m) (2007 & 2008)
904
901
907
906
919
903
902
905
908
0.2
0.4
0.6
0.8
1.0
1.2
1.4
10
20
30
40

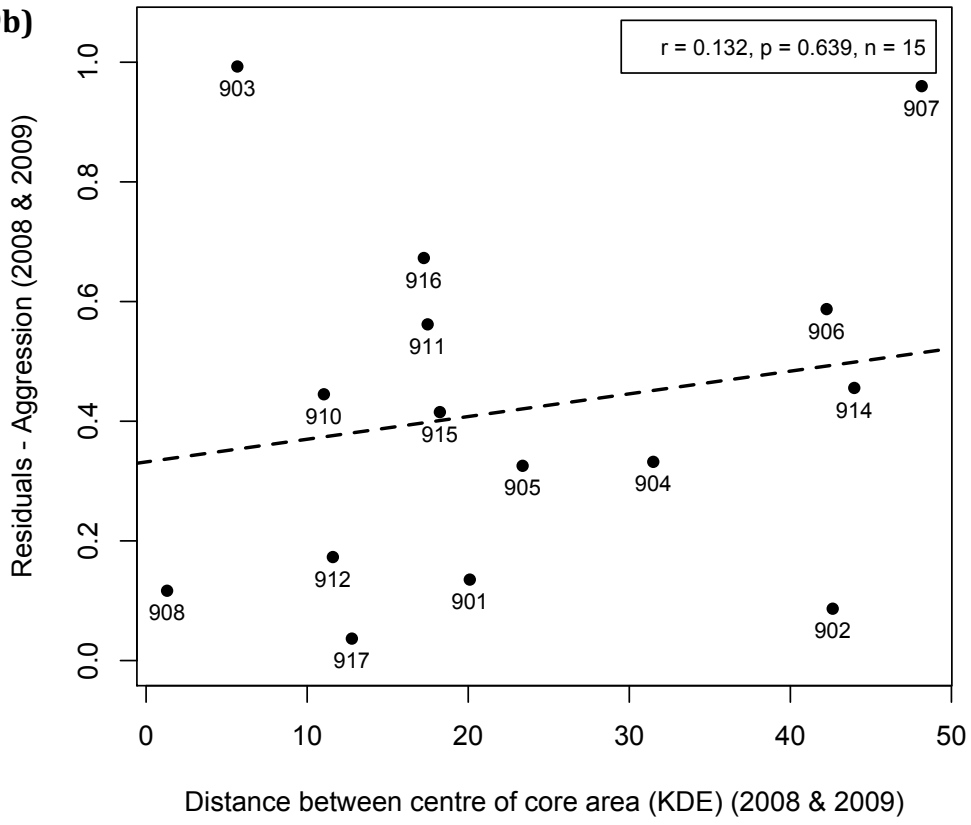
A4.8b)


r = 0.5, p = 0.178, n = 9
Residuals - Aggression (2007 & 2008)
Distance between centre of core area (KDE) (2007 & 2008)
904
901
907
906
903
919
908
902
905
0.2
0.4
0.6
0.8
1.0
1.2
1.4
10
20
30
40

A4.9a)


r = 0.332, p = 0.226, n = 15
Residuals - Aggression (2008 & 2009)
Distance between pupping sites (m) (2008 & 2009)
0.0
0.2
0.4
0.6
0.8
1.0
10
20
30
40
50
903
907
916
911
906
910
915
914
904
905
912
901
908
902
917

A4.9b)


r = 0.132, p = 0.639, n = 15
Residuals - Aggression (2008 & 2009)
Distance between centre of core area (KDE) (2008 & 2009)
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
903
907
916
911
906
910
914
915
905
904
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902
917

Chapter 5: Appendix

Section A:

The beta-binomial distribution

The beta-binomial distribution is a compound distribution of the binomial distribution with the Beta distribution, which allows for heterogeneity in per-trial probability (Crowder, 1979; Bolker, 2008). In this section both the binomial and Beta distributions are briefly discussed as a prelude to the beta-binomial distribution and its application in ecological studies. The binomial distribution assumes that the probability (*p*) of the behaviour occurring (*k*) given *n* scan samples (trials) is the same:

$$P(k \mid n,p) = \binom{n}{k} p^k (1-p)^{n-k} \qquad \text{(Eq. 1)}$$

However, for the binomial distribution, when the probability (*p*) of the behaviour occurring varies between scan samples (*n*), the variance quickly exceeds the mean, resulting in overdispersed data (Layton & Siikamaki, 2009). One approach to dealing with overdispersion is to use a compound probability distribution to characterise the variation in *p* (Richards, 2008). Therefore, we assume that the probability of the behaviour occurring is randomly distributed, which can be described using the Beta distribution:

$$f(p;\alpha,\beta) = \frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)} p^{\alpha-1}(1-p)^{\beta-1} \qquad \text{(Eq. 2)}$$

where Γ is the Gamma function. This distribution is constrained between 0 and 1 and is flexible, depending on α and β (which describe the Beta distribution of the probability of a behaviour occurring during a scan sample (*n*)). This distribution can take on many different shapes, including unimodal, bimodal, convex and concave. For example, when $\alpha < \beta$ the peak shifts towards 0 and when $\beta < \alpha$ the peak shifts towards 1 (Bolker, 2008; Layton & Siikamaki, 2009). Therefore, given the flexibility of the Beta distribution, it is often used in studies where the probability of recording an event is relatively rare (Ryan, 2007).

The probability of a behaviour occurring given α, β, and *n*, is calculated by integrating the binomial (Eq. 1) and the Beta (Eq. 2) distributions, and thus producing the beta-binomial distribution:

$$f(k|,\alpha,\beta) = \frac{\Gamma(n+1)\Gamma(\alpha+\beta)\Gamma(\beta+n-k)\Gamma(\alpha+\beta)}{\Gamma(k+1)\Gamma(n-k+1)\Gamma(\alpha+\beta+n)\Gamma(\alpha)\Gamma(\beta)} \qquad \text{(Eq. 3)}$$

When $\alpha = \beta = 1$ the probability of a behaviour occurring during a scan sample (*n*) is equally likely to be any value between 0 and 1, and the beta-binomial gives a uniform (discrete) distribution between 0 and *N*, where *N* is the number of scan samples per hour. As $\alpha + \beta$ increases, the variance of the underlying heterogeneity decreases and the beta-binomial converges to the binomial distribution (Bolker, 2008; Richards, 2008).

The beta-binomial distribution has been applied in a number of ecological studies (Zarnoch et al., 1995; Harun et al., 1999; Diserud & Odegaard, 2000; Shiyomi et al., 2000; Tsutsuni et al., 2001; Shiyomi et al., 2002; Chen et al., 2006; Thurow et al., 2006; Ryan, 2007; Chen et al., 2008; Wolf & Mangel, 2008; Layton & Siikamaki, 2009; Richards et al., 2009; Schauber et al., 2009). Ultimately, the benefits of the beta-binomial distribution are that it allows variability in the underlying probabilities per scan sample (*n*). Therefore, the beta-binomial distribution always has more spread (variance) than the equivalent binomial distribution, because the Beta distribution adds uncertainty to the probability (Harun et al., 1999; Wolf & Mangel, 2008). Thus, when a binomial distribution does not match observations, because the observations exhibit too much spread, a beta-binomial distribution is often used instead (Bolker, 2008; Richards, 2008).

Section B:

A brief review of model selection and multi-model inference using Akaike's Information Criterion

Introduction

Model selection and multi-model inference using information theoretic (IT) approaches have been widely promoted in recent years (Hilborn & Mangel, 1997; Burnhan & Anderson, 2002; Garamszegi, 2011). IT methods represent a different approach to inference than that of the classical null hypothesis significance testing (NHST) approach. The IT approach recognises that data seldom provide absolute support for a single hypothesis; rather, the data available can only influence the extent to which the researcher considers any given hypothesis to be supported (relative to competing explanations; Richards et al., 2011). The most commonly used IT method is Akaike's Information Criterion (AIC; Burnham & Anderson, 2002; Burnham et al., 2011). IT-AIC was developed by Akaike (1973, 1974) and is based on deep theoretical foundations that have been discussed elsewhere (see Anderson et al., 2000 and Burnham & Anderson, 2002). However, in practice the concept is simple, the model with the lowest AIC is selected as the 'best' model for the data available. It is not a test in itself; it is an approach that allows the comparison of multiple hypotheses (models), with no single hypothesis made to be the null (Anderson et al., 2000). Consequently, IT-AIC has been referred to as the 'hard thinking' approach (Steidl, 2006; Burnham et al., 2011), because researchers are required to think about alternative hypotheses. In contrast, the NHST approach provides a research hypothesis that is compared with a competing, usually trivial, null hypothesis (Burnham et al., 2011).

AIC and model selection

A complete understanding of the mathematical foundations of AIC are not a necessary prerequisite in order to successfully apply and interpret IT-AIC. Nevertheless, in order to understand how AIC treats the parameters included in the model, it is important to have a basic underlying knowledge as to how AIC is calculated. AIC is defined as:

$$AIC = -2\log(\ell(\hat{\theta}|y)) + 2K \quad \text{(Eq. 1)}$$

where $\log(\ell(\hat{\theta}|y))$ is the value of the maximised log-likelihood over the unknown parameters (θ), given the data (y) and the model, and K is the number of parameters estimated in the model (Anderson et al., 2000; Burnham & Anderson, 2002). The first term on the right-hand side tends to decrease as more parameters are added, whilst the second term ($2K$) gets larger as more parameters are added. There is also a second order variant of AIC (referred to as AICc), which is recommended over AIC when there are too many parameters in relation to the size of the sample (Burnham & Anderson, 2002). AICc is defined as:

$$AICc = AIC + \frac{2K(K+1)}{n-K-1} \quad \text{(Eq. 2)}$$

Where n is the sample size. The difference between AIC and AICc is that the latter has an additional bias-corrected term. Burnham & Anderson (2002) recommend using AICc over AIC if the ratio n/K is small (< 40). However, if n is large with respect to K, then the difference between AIC and AICc will be negligible. Therefore, in an effort to be conservative, some researchers recommend that AICc is used as the default, rather than AIC (Burnham & Anderson, 2002; Burnham et al., 2011; Grueber et al., 2011). The bias-correcting terms in AIC and AICc represent the trade-off between bias and variance or, in other words, the trade-off between underfitting and overfitting the model, which is a fundamental concept in the principal of parsimony (Burnham & Anderson, 2002). Both AIC and AICc are used in the same manner in model selection and model inference; consequently, the term AIC will be used throughout, but it should be considered synonymous with AICc unless otherwise stated.

The model having the lowest AIC value may be deemed as the most parsimonious model (often referred to as the 'best' model); however, AIC is only an estimate of model parsimony, another model having a higher AIC value may in fact be the more parsimonious (Anderson et al., 2000; Burnham & Anderson 2002; Richards, 2005). Consequently, it is considered poor practice to focus

interpretation exclusively on the 'best' AIC model; this is particularly true when other models are nearly as well supported as the 'best' model (Burnham & Anderson, 2001; Burnham & Anderson, 2002; Bolker, 2008). Instead, it should be acknowledged that a number of models could share similar levels of support. These models are often referred to as 'the confidence set', and various selection rules have been proposed to define which models should be retained within the confidence set (Anderson et al., 2000; Burnham & Anderson, 2002; Richards, 2005; Richards, 2008; Bolker et al., 2009).

The selection rules are based on the $\triangle$ value, which is defined as the difference between the AIC of the model with the lowest AIC ($\triangle = 0$) and that of the competing model(s). The 'traditional' reference for an IT-AIC rule of thumb for model selection is Burnham & Anderson (2002). They stated that all models with a $\triangle$ value of < 2 should be used for inference; models with a $\triangle$ value between about 4 and 7 are less likely to be the best model but probably should not be discounted; and models with a $\triangle$ value > 10 are extremely unlikely to be the best model and can be discounted. However, more recently Burnham et al. (2011) have revised this rule of thumb stating that "models where $\triangle$ is in the 2 - 7 range have some support and should rarely be dismissed".

Richards (2008) and Richards et al. (2011) have argued that both the original and revised rule of thumb could be problematic, as it may result in the selection of overly complex models. They deem that the additional covariate(s) within complex models provide little or no increase in fit compared to simpler 'nested' models with a lower $\triangle$ value (i.e. both models contain the same terms but the more complex model has at least one additional term; Burnham & Anderson, 2002; Richards, 2008; Richards et al., 2011). In this scenario both models will have near equivalent maximum likelihood and as a consequence, the more complex model will have a $\triangle$ value equal to, or slightly less than 2 (given that the addition of one estimable parameter will increase AIC by 2; Eq 1). In such a case, there is no sense selecting the more complex model and making inference from it, as nothing is explained by the additional complexity (Richards, 2008).

Similar to Burnham & Anderson's (2002) and Burnham et al.'s (2011) rule of thumb, Richards (2005, 2008) and Richards et al. (2011) suggest that all models

having a $\triangle$ value < 6 should be retained in the confidence set. They also advocate an additional rule of thumb whereby models should only be retained if their $\triangle$ value is less than that of all its simpler nested models. This approach of omitting more complex nested models from the confidence set, if they provide a minimal increase in fit, has also been suggested by Burnham & Anderson (2002), and more recently by Grueber et al. (2011). Furthermore, this approach is commonly used when selecting models within a Bayesian framework (Madigan & Raftery 1994). Therefore, it is not a new methodological concept with respect to model selection using an IT approach.

Incorrectly selecting overly complex models and failure to select the most parsimonious simpler model is likely to occur when the true effect of a measured covariate is quite weak, data are few and/or the data are overdispersed. Therefore, as a cost for using this more conservative rule of thumb, there is a reduced chance of selecting the true best model, especially when it is particularly complex (Richards, 2008). However, using simulated data, where the true best model was known, Richards (2008) showed that in cases where the best model was not selected, the rule always selected the more conservative second-best model. The principal benefits of this more conservative approach is that it reduces the likelihood of selecting overly complex models, which is a common criticism of AIC (Johnson & Omland, 2004) and, as a consequence the confidence set is more likely to be comprised of fewer and simpler models.

The likelihood of retaining complex models within the confidence set is also increased if interaction terms are included within the global model (Schielzeth, 2010; Garamszegi, 2011; Mundry, 2011). Criticism over the inclusion of interaction terms is growing, particularly when interactions with three or more covariates are considered (Mundry, 2011). Even with two covariates some still consider interactions to be very difficult to interpret biologically (Hector et al., 2010; Schielzeth, 2010; Mundry, 2011) and, depending on the number of interactions included, testing every model within the global model could be computationally impossible (Hector et al., 2010). Furthermore, if all interaction terms that were considered biologically possible were included, then there would be an increased risk of overfitting the data to the model. Consequently, this increases the likelihood of complex models being retained within the confidence set (Schielzeth, 2010;

Mundry, 2011). There is no rule of thumb for whether or not interactions should or should not be included in the global model. However, if they are included there should be a biologically sound reason for doing so, and the resulting output has to be biologically meaningful (Schielzeth, 2010).

Approaches to multi-model inference

Inference is made using the models contained within the confidence set; this is typically referred to as multi-model inference (Burnham & Anderson, 2002). One approach to multi-model inference is model averaging. For this approach the model weights (often referred to as Akaike weights) are used (see Burnham & Anderson, 2002 & Lukacs et al., 2007 for details on how model weights are calculated). Some regard these weights as probabilities because each is within the interval [0,1] and they sum to 1 (Burnham et al., 2011). Consequently, these researchers refer to model weights as the 'weight of evidence' in favour of model *x* being the true best model within the confidence set (Burnham & Anderson, 2001; Burnham & Anderson, 2002; Lukacs et al., 2007). However, others consider them to have no probability interpretation, but do suggest that they can be useful for multi-model inference (Bolker, 2008). As a rule of thumb, it has been suggested that if the 'best' model has a weight of < 0.9 then model averaging should be used (Burnham & Anderson, 2002; Grueber et al., 2011). It is important to note that all advocates of this approach state that the full set of *a priori* models should be used in model averaging (Burnham & Anderson, 2002; Grueber et al., 2011; Symonds & Moussalli, 2011). In other words, irrespective of the rule of thumb used to define the confidence set, the weights of the models within the confidence set must be calculated using all of the competing models.

There are two approaches to model averaging: the natural average method and the zero method (also referred to as full-model averaging; Burnham & Anderson, 2002; Lukacs et al., 2007; Grueber et al., 2011; Nakagawa & Freckleton, 2011). The natural average method takes the parameter estimate for each covariate and averages it over the models in which that covariate appears. It is then weighted by the summed weights of these models. Alternatively, the zero method substitutes a parameter estimate of zero where the given covariate is not included in a model. Therefore, the parameter estimate is obtained by averaging

over all models, which means that the zero method decreases the effect sizes of covariates that only appear in models with small weights. Irrespective of the method used, the covariate with the largest weight is considered to be the most important, whilst the covariate with the smallest weight is deemed to be the least important (Burnham & Anderson, 2001).

Despite the majority of researchers agreeing that model weights are a useful tool in multi-model inference, there are inconsistencies in the way in which model weights are used (Grueber et al., 2011; Symonds & Moussalli, 2011). One of the principal concerns is that the natural average and zero methods typically give very contrasting results (Grueber et al., 2011; Symonds & Moussalli, 2011) and although researchers have offered suggestions (Nakagawa & Freckleton, 2011; Symonds & Moussalli, 2011), there are no clear guidelines on which method is the most suitable to apply in a given scenario. Consequently, most acknowledge that further research into the use(s) of model weights in multi-model inference is required (Burnham & Anderson, 2002; Grueber et al., 2011). Conversely, there are some researchers, such as Richards (2005) and Richards et al. (2011) who argue that model weights are likely to be relatively uninformative indicators of the true best model. In the case of Richards et al. (2011), they supported their argument by using simulated datasets. They showed that, if a true difference between the means of the distributions from which two samples were drawn did occur, then making inference on the AIC 'best' model was likely to be more accurate, on average, than using model averaging. Richards et al. (2011) also noted that model weights ignore nested models, which could lead to overestimating the support given to complex models. This issue is not easily dealt with given the consensus that all potential models within the global model should be used in order to obtain accurate model weights (Burnham & Anderson, 2002; Grueber et al., 2011; Symonds & Moussalli, 2011). Therefore, Richards et al. (2011) argue that there are "no great advantages arising from using model weights in AIC analyses". Consequently, they advocate a "cautionary approach" of basing inference on the simpler models within the confidence set.

The pitfalls of IT-AIC approaches

It should be noted that there is a difference of opinion as to what can be gained from converting to an IT approach over a NHST approach for simple analyses (Lukacs et al., 2007; Richards et al., 2011). However, for problems of more complex causality many researchers consider IT approaches to offer considerable advantages (Burnham & Anderson, 2002; Richards, 2005; Richards et al., 2011). With respect to AIC, there are some researchers that have taken a more cautious and/or sceptical approach (Stephens et al., 2005; Stephens et al., 2007; Mundry, 2011). For the most part their concerns relate to the misuse and/or misinterpretation of AIC. However, researchers that strongly advocate the use of AIC also share the majority of these concerns (Burnham & Anderson, 2002; Burnham et al., 2011), which include the use of stepwise regression (Whittingham et al., 2006; Hegyi & Garamszegi, 2011) and model 'dredging' (Anderson & Burnham, 2002; Burnham et al., 2011; Dochtermann & Jenkins 2011).

Stepwise regression usually uses NHST and typically involves starting with the global model and removing the least significant covariate until all covariates within the model are significant (Whittingham et al., 2006; Hegyi & Garamszegi, 2011). More recently, statistical software packages now implement a 'stepwise AIC' procedure, and thus make this approach more accessible to researchers using AIC. For example, the step() function in R tests which covariate, when added to the model, gives the highest AIC value. Consequently, this covariate is omitted from the model and the process is repeated until it is not possible to omit a covariate without increasing the AIC value. Therefore, stepwise regression does not test every possible model within the global model, and as a consequence it is not possible to make multi-model inference (Whittingham et al., 2006; Burnham et al., 2011; Hegyi & Garamszegi, 2011).

Model 'dredging' occurs when all of the possible covariates collected are included in the global model and every possible combination of those variables is modelled (Burnham & Anderson, 2002). The subtle point with respect to avoiding stepwise regression and model dredging is that the global model should consist of covariates that are thought (or are known) to be biologically important, and all models within the global model should be compared. Consequently, both stepwise

regression and model dredging are heavily criticised because both approaches require no thought with respect to the hypotheses formed. Therefore, these approaches bypass the “hard thinking” step, which is arguably one of the principal benefits of using AIC for model selection and inference (Steidl, 2006; Burnham et al., 2011).

Conclusion

“Deciding what models to use and how to use them is fundamentally difficult” (Bolker, 2008, p217). Consequently, it is important to consider the questions posed and remember that modelling is a method used to test hypotheses that have been formed based on current knowledge of the ecological system under study. Therefore, from an ecologist’s point of view (rather than a statistician’s point of view, for example), basing ecological inference on the simplest models selected, whilst giving less support to covariates included in fewer, more complex models does make biological sense. Arguably, the major issue with this approach is the growing number of researchers modelling ecological datasets that they have not collected themselves and do not have first-hand experience with the system in which they are modelling. Therefore, under these circumstances it may become increasingly difficult to apply biological understanding to model inference, especially if there is little empirical research published on the study system being modelled.

Table A5.1: To ascertain whether or not the selected behavioural categories (see Section 5.3.1) were zero-inflated, each of the four behavioural categories for each of the nine datasets were modelled using a binomial (B; 2 d.f.) and a beta-binomial (BB; 3 d.f.; Appendix, Section A) distribution (Bolker, 2008, p283 - 289). These models were compared using AICc (Section 5.3.5; Appendix, Section B). The table presents these models and ranks them based on their △ value; the BB distributions are in bold. In general, the analyses showed that the BB distribution was more often than not the 'best' distribution (the model with the lowest AICc). Where this was not the case, the BB distribution rarely had a △ > 3. Following the protocol suggested by Bolker (2008), these distributions were also applied to the global model (a model which contains all of the covariates of interest) and the 'best' model (the model with the lowest AICc as judged by the BB distribution), to ascertain which of the two distributions best fitted the data once the covariates were included in the model; See Table A5.2 for these analyses.

	2007 – 2009						**2007 & 2008**				**2008 & 2009**				**2007 & 2009**			
	2007		**2008**		**2009**		**2007**		**2008**		**2008**		**2009**		**2007**		**2009**	
Behaviour	**Dist.**	△	**Dist.**	△	**Dist.**	△	**Dist.**	△	**Dist.**	△	**Dist.**	△	**Dist.**	△	**Dist.**	△	**Dist.**	△
Alert	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**
	B	30.4	B	75.9	B	43.7	B	31.2	B	93.5	B	156.6	B	160.1	B	33.5	B	53.3
Pup Check	B	0	B	0	B	0	B	0	B	0	**BB**	**0**	**BB**	**0**	B	0	B	0
	BB	**2.3**	**BB**	**2.6**	**BB**	**2**	**BB**	**1.4**	**BB**	**1.4**	B	11	B	18.4	**BB**	**3**	**BB**	**2.2**
Aggression	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**
	B	6.8	B	81.3	B	2	B	7.9	B	82.2	B	110.9	B	9.3	B	7.7	B	19
Locomotion	B	0	B	0	**BB**	**0**	B	0	B	0	B	0	**BB**	**0**	B	0	**BB**	**0**
	BB	**4.1**	**BB**	**4.8**	B	7.8	**BB**	**3.9**	**BB**	**6.2**	**BB**	**3.3**	B	13.8	**BB**	**3.6**	B	9.4

Table A5.2: Using the beta-binomial (BB) and the binomial (B) distribution, the difference between the AICc for the global model and the 'best' model are shown. The BB distribution was used to define the 'best' model (Table A5.1) and the B distribution was applied to the same model to ascertain if the additional binomial variance was required (Prentice, 1986; Harun et al., 1999; Bolker, 2008). Results in bold italics indicate that the B distribution was the 'best' model; the converse is true for the standard text. Grey cells indicate that data were collected but were insufficient (see Section 5.4); black cells indicate that there are no data for that particular analysis. Where the B is the 'best' distribution the difference between the BB distribution was typically $\triangle \leq 2$. The inclusion of the additional binomial variation provided by the BB distribution increases AIC by 2 (Appendix, Section B, Eq. 1) and the AICc has an additional bias-corrected term, which can potentially increase this 'penalty' (Appendix, Section B, Eq. 2). Therefore, the negligible difference in the $\triangle$ values where the B distribution is the 'best' model is effectively the difference between including the additional term in the model. To test this, the B distribution was applied to the global model for each of these datasets to ascertain whether or not the 'best' model for the B distribution was the same (i.e. retained the same covariates) as the 'best' model for the BB distribution, and as expected, it was (results not presented). Therefore, to maintain consistency with respect to the analytical approach used for each of the behavioural categories and for each of the datasets, the BB distribution was applied to all models.

		Years					
		2007		**2008**		**2009**	
Behaviour	**Analyses**	**Global**	**Best**	**Global**	**Best**	**Global**	**Best**
Alert	2007 - 2009	15.571	17.381	40.171	45.187	13.684	17.001
Pup Check		***2.017***	***1.877***	***2.27***	***1.016***	***2.091***	***1.834***
Aggression				60.85	60.158	***2.056***	***1.109***
Locomotion				***2.188***	***2***	5.494	0.052
Alert	2007 & 2008	14.654	16.164	47.426	53.064		
Pup Check		***2.016***	***1.89***	***1.647***	***0.433***		
Aggression				60.455	59.7		
Locomotion				***2.126***	***2.003***		
Alert	2008 & 2009			76.096	82.086	74.694	77.814
Pup Check				***0.135***	0.834	***0.056***	0.199
Aggression				83.339	83.199	4.446	7.79
Locomotion				***2.116***	***1.647***	1.506	9.625
Alert	2007 & 2009	18.977	21.773			20.937	23.408
Pup Check		***2.053***	***2.008***			***2.2***	***1.78***
Aggression						1.263	8.469
Locomotion						0.492	6.473

Table A5.3: The relationship between the four response variables and each of the covariates for individuals re-sighted in all three years (n = 8). The analyses were conducted using a Spearman's rank correlation coefficient; significant (p < 0.05) values are in bold. RV = response variable; CV = covariate; see the footnote for the definition of each of the covariates.

		2007		2008		2009	
RV	CV	*p*	r	*p*	r	*p*	r
Alert	ACT	**<0.001**	**0.168**	**<0.001**	**0.246**	**<0.001**	**0.219**
	DEN	**<0.001**	**0.145**	0.593	-0.018	0.388	0.031
	PUP	0.521	-0.027	0.8928	0.004	**0.01**	**-0.092**
	POOL	0.109	0.067	0.33	0.033	0.047	0.071
	HOME	0.107	0.067	0.819	0.008	**<0.001**	**-0.146**
	RAIN	0.61	0.021	0.121	-0.052	0.961	-0.002
	TEMP	0.836	0.009	0.239	-0.039	0.766	-0.011
	AGE	0.067	-0.076	0.793	0.009	0.685	0.015
	NFN	0.984	0.001	0.444	0.026	0.895	0.005
Pup Check	ACT	**<0.001**	**0.213**	**<0.001**	**0.166**	**<0.001**	**0.194**
	DEN	0.431	0.033	0.576	-0.019	0.843	0.007
	PUP	0.172	0.057	0.893	-0.004	0.398	-0.03
	POOL	0.982	0.001	0.073	0.06	**0.002**	**0.109**
	HOME	0.692	-0.017	0.234	-0.04	**0.029**	**-0.078**
	RAIN	0.6	0.022	0.46	-0.025	0.57	0.02
	TEMP	0.368	-0.038	0.217	0.041	0.2	-0.046
	AGE	0.412	-0.034	**0.018**	**-0.079**	0.143	-0.052
	NFN	0.381	-0.037	0.536	0.021	0.784	0.01
Locomotion	ACT	**0.008**	**0.111**	**<0.001**	**0.144**	**<0.001**	**0.143**
	DEN	0.226	-0.051	0.528	0.021	0.876	0.006
	PUP	0.652	0.019	0.871	0.005	0.4	0.03
	POOL	**0.032**	**0.09**	0.961	-0.002	0.234	0.043
	HOME	**0.01**	**-0.108**	0.355	-0.031	**<0.001**	**-0.121**
	RAIN	0.072	0.075	0.374	0.03	0.124	0.055
	TEMP	0.965	0.002	0.995	0	0.853	0.007
	AGE	0.201	-0.054	0.076	-0.059	**0.039**	**-0.074**
	NFN	0.08	0.079	0.617	-0.017	0.917	-0.004
Aggression	ACT	**<0.001**	**0.168**	**<0.001**	**0.246**	**<0.001**	**0.219**
	DEN	**<0.001**	**0.145**	0.593	-0.018	0.3882	0.031
	PUP	0.521	-0.027	0.894	0.004	**0.01**	**-0.092**
	POOL	0.109	0.067	0.33	0.033	**0.047**	**0.071**
	HOME	0.107	0.067	0.819	0.008	**<0.001**	**-0.146**
	RAIN	0.61	0.021	0.121	-0.052	0.961	-0.002
	TEMP	0.836	0.009	0.239	-0.039	0.766	-0.011
	AGE	0.067	-0.076	0.793	0.009	0.685	0.015
	NFN	0.984	0.001	0.444	0.026	0.895	0.005

ACT: proportion of time the pup spent active; **DEN**: the number of females within a 10m buffer zone of the mother; **POOL**: the distance between a mother and her nearest pool (m); **HOME**: the location of the female within her estimated home range (Kernel Density Estimate) the higher the number, the closer the female was to the centre of her core area; **RAIN**: the volume of rain that fell from the end of observations on day *x* and the end of observations on day *x*+1 (mm); **TEMP**: air temperature (^{o}C); **AGE**: the age of the mothers' pup calculated as days postpartum; **NFN**: the distance between a mother and her nearest female neighbour (m).

Table A5.4: The relationship between the four response variables and each of the covariates for individuals re-sighted in 2007 & 2008 (n = 9). The analyses were conducted using a Spearman's rank correlation coefficient; significant ($p < 0.05$) values are in bold. RV = response variable; CV = covariate. The definition of each of the covariates is shown in the footnote of Table A5.3.

		2007		2008	
RV	CV	*p*	r	*p*	r
Alert	ACT	**<0.001**	**0.146**	**<0.001**	**0.236**
	DEN	**<0.001**	**0.143**	0.494	0.022
	PUP	0.439	-0.03	0.469	-0.023
	POOL	0.126	0.06	0.134	0.048
	HOME	0.16	0.055	0.198	0.041
	RAIN	0.73	0.014	0.051	-0.062
	TEMP	0.934	0.003	0.234	-0.038
	AGE	0.082	-0.068	0.206	0.041
	NFN	0.639	-0.018	0.596	0.017
Pup Check	ACT	**<0.001**	**0.213**	**<0.001**	**0.167**
	DEN	0.116	0.062	0.854	-0.006
	PUP	0.326	0.039	0.669	-0.014
	POOL	0.879	-0.006	0.084	0.0554
	HOME	0.558	-0.023	0.254	-0.037
	RAIN	0.575	0.022	0.62	-0.016
	TEMP	0.372	-0.035	0.113	0.051
	AGE	0.376	-0.035	**0.033**	**-0.068**
	NFN	0.146	-0.057	0.572	0.018
Locomotion	ACT	**<0.001**	**0.108**	**<0.001**	**0.14**
	DEN	0.559	-0.023	0.367	0.029
	PUP	0.728	0.014	0.861	-0.006
	POOL	**0.035**	**0.083**	0.922	0.003
	HOME	**0.007**	**-0.105**	0.286	-0.034
	RAIN	0.074	0.07	0.351	0.03
	TEMP	0.874	0.006	0.88	-0.005
	AGE	0.219	-0.048	0.1	-0.053
	NFN	0.146	0.057	0.716	-0.012
Aggression	ACT	**0.012**	**0.099**	**0.006**	**0.088**
	DEN	**0.029**	**0.086**	**0.016**	**0.077**
	PUP	0.483	0.28	0.224	0.039
	POOL	0.994	0	0.082	-0.056
	HOME	0.547	-0.024	0.613	0.016
	RAIN	0.332	0.038	0.813	0.008
	TEMP	0.695	-0.015	0.114	0.051
	AGE	0.906	0.005	0.245	0.037
	NFN	0.416	-0.032	0.137	-0.048

Table A5.5: The relationship between the four response variables and each of the covariates for individuals re-sighted in 2008 & 2009 (n =15). The analyses were conducted using a Spearman's rank correlation coefficient; significant ($p < 0.05$) values are in bold. RV = response variable; CV = covariate. The definition of each of the covariates is shown in the footnote of Table A5.3.

		2008		2009	
RV	CV	*p*	r	*p*	r
Alert	ACT	**<0.001**	**0.257**	**<0.001**	**0.226**
	DEN	0.717	-0.009	0.466	-0.019
	PUP	0.428	0.019	**0.004**	**-0.074**
	POOL	0.672	0.01	**<0.001**	**0.096**
	HOME	0.058	-0.047	**<0.001**	**-0.152**
	RAIN	0.143	-0.036	0.07	0.047
	TEMP	0.841	-0.005	0.174	-0.035
	AGE	0.634	-0.012	0.249	-0.03
	NFN	0.132	0.037	0.197	0.033
Pup Check	ACT	**<0.001**	**0.206**	**<0.001**	**0.185**
	DEN	0.636	0.012	**0.044**	**-0.052**
	PUP	0.264	0.264	0.929	0.002
	POOL	0.762	0.007	0.217	0.032
	HOME	0.456	-0.018	**<0.001**	**-0.1**
	RAIN	0.277	-0.027	**0.006**	**0.071**
	TEMP	**0.001**	**0.078**	0.069	-0.047
	AGE	0.055	-0.047	**0.043**	**-0.052**
	NFN	0.71	0.009	**0.028**	**0.057**
Locomotion	ACT	**<0.001**	**0.153**	**<0.001**	**0.158**
	DEN	0.97	0	0.346	-0.024
	PUP	0.71	-0.009	0.742	0.009
	POOL	0.873	0.004	0.055	0.05
	HOME	0.077	-0.044	**<0.001**	**-0.107**
	RAIN	0.276	0.027	**0.027**	**0.057**
	TEMP	0.671	0.01	**0.05**	**-0.051**
	AGE	**0.032**	**-0.053**	**0.02**	**-0.06**
	NFN	0.919	-0.003	0.643	0.012
Aggression	ACT	**<0.001**	**0.088**	**0.01**	**0.067**
	DEN	**0.002**	**0.076**	**0.019**	**0.061**
	PUP	0.458	0.018	**0.032**	**0.056**
	POOL	**0.029**	**-0.054**	**0.006**	**0.071**
	HOME	0.195	0.032	0.238	-0.031
	RAIN	0.869	-0.004	0.213	-0.032
	TEMP	0.082	0.043	0.706	-0.01
	AGE	0.251	0.028	0.552	0.015
	NFN	**0.04**	**-0.051**	**0.001**	**-0.083**

Table A5.6: The relationship between the four response variables and each of the covariates for individuals re-sighted in 2007 & 2009 (n = 9). The analyses were conducted using a Spearman's rank correlation coefficient; significant ($p < 0.05$) values are in bold. RV = response variable; CV = covariate. The definition of each of the covariates is shown in the footnote of Table A5.3.

		2007		2009	
RV	CV	*p*	r	*p*	r
Alert	ACT	**<0.001**	**0.158**	**<0.001**	**0.207**
	DEN	**<0.001**	**0.136**	0.275	0.037
	PUP	0.428	-0.032	**<0.001**	**-0.115**
	POOL	0.147	0.058	0.088	0.058
	HOME	0.142	0.059	**0.004**	**-0.098**
	RAIN	0.662	0.017	0.877	0.005
	TEMP	**0.012**	**0.758**	-0.019	0.574
	AGE	0.059	-0.075	0.333	0.033
	NFN	0.901	-0.005	0.782	-0.009
Pup Check	ACT	**<0.001**	**0.199**	**<0.001**	**0.2**
	DEN	0.522	0.026	0.79	0.009
	PUP	0.268	0.044	0.255	-0.038
	POOL	0.807	0.01	**0.003**	**0.1**
	HOME	0.528	-0.025	0.116	-0.053
	RAIN	0.5	0.027	0.158	0.048
	TEMP	0.227	-0.048	0.106	-0.055
	AGE	0.378	-0.035	0.411	-0.028
	NFN	0.479	-0.028	0.52	0.022
Locomotion	ACT	**0.004**	**0.113**	**<0.001**	**0.134**
	DEN	0.158	-0.056	0.438	0.026
	PUP	0.947	0.003	0.163	0.047
	POOL	**0.015**	**0.097**	0.541	0.021
	HOME	**0.005**	**-0.112**	**<0.001**	**-0.125**
	RAIN	0.052	0.077	0.258	0.038
	TEMP	0.821	0.009	0.846	-0.007
	AGE	0.182	-0.053	**0.016**	**-0.081**
	NFN	0.072	0.072	0.368	-0.03
Aggression	ACT	**0.008**	**0.106**	**0.033**	**0.072**
	DEN	**0.034**	**0.085**	0.454	0.025
	PUP	0.594	0.021	**0.009**	**0.088**
	POOL	0.865	0.007	0.978	0
	HOME	0.391	-0.034	0.152	-0.048
	RAIN	0.409	0.033	0.446	-0.026
	TEMP	0.875	-0.006	0.54	-0.021
	AGE	1	0	0.672	-0.014
	NFN	0.354	-0.037	0.154	-0.048

Table A5.7: The number of models retained (from a possible 127) at each of the 5 stages of model selection (Section 5.3.6), for each of the behavioural categories, for each of the 4 analyses. Stage 1: models within a $\triangle < 6$; stage 2: after considering nested models; stage 3: redefining models after considering collinearity; stage 4: models within a $\triangle < 6$; stage 5: after considering nested models; see Section 5.3.6 for a more detailed account of the model selection protocol. *Indicates that none of the models within the confidence set contained collinear covariates. Grey cells indicate that data were collected but were insufficient (see Section 5.4); black cells indicate that there are no data for that particular analysis.

		Stage 1			Stage 2			Stage 3			Stage 4			Stage 5		
Behaviour	Years present	2007	2008	2009	2007	2008	2009	2007	2008	2009	2007	2008	2009	2007	2008	2009
Alert	2007 – 2009	26	22	15	2	7	1	2*	15	5	2	3	1	2	3	1
	2007 & 2008	26	22		3	10		3*	17		3	3		3	3	
	2008 & 2009		27	22		13	4		19	9		3	3		3	2
	2007 & 2009	34		17	6		3	15		7	8		2	5		1
Pup Check	2007 – 2009	30	30	17	1	2	2	1*	2*	7	1	2	1	1	2	1
	2007 & 2008	30	30		2	2		2*	2*		2	2		2	2	
	2008 & 2009		32	28		5	6		9	11		2	3		2	3
	2007 & 2009	33		41	2		6	2*		13	2		7	2		3
Locomotion	2007 – 2009		26	13		1	2		1*	7		1	5		1	2
	2007 & 2008		24			2			5			1			1	
	2008 & 2009		16	13		2	2		5	7		1	2		1	1
	2007 & 2009			11			2			7			4			3
Aggression	2007 – 2009		43	31		3	3		3*	5		3	4		3	2
	2007 & 2008		53			4			4*			4			4	
	2008 & 2009		37	23		6	5		9	9		6	4		5	3
	2007 & 2009			51			2			5			5			4

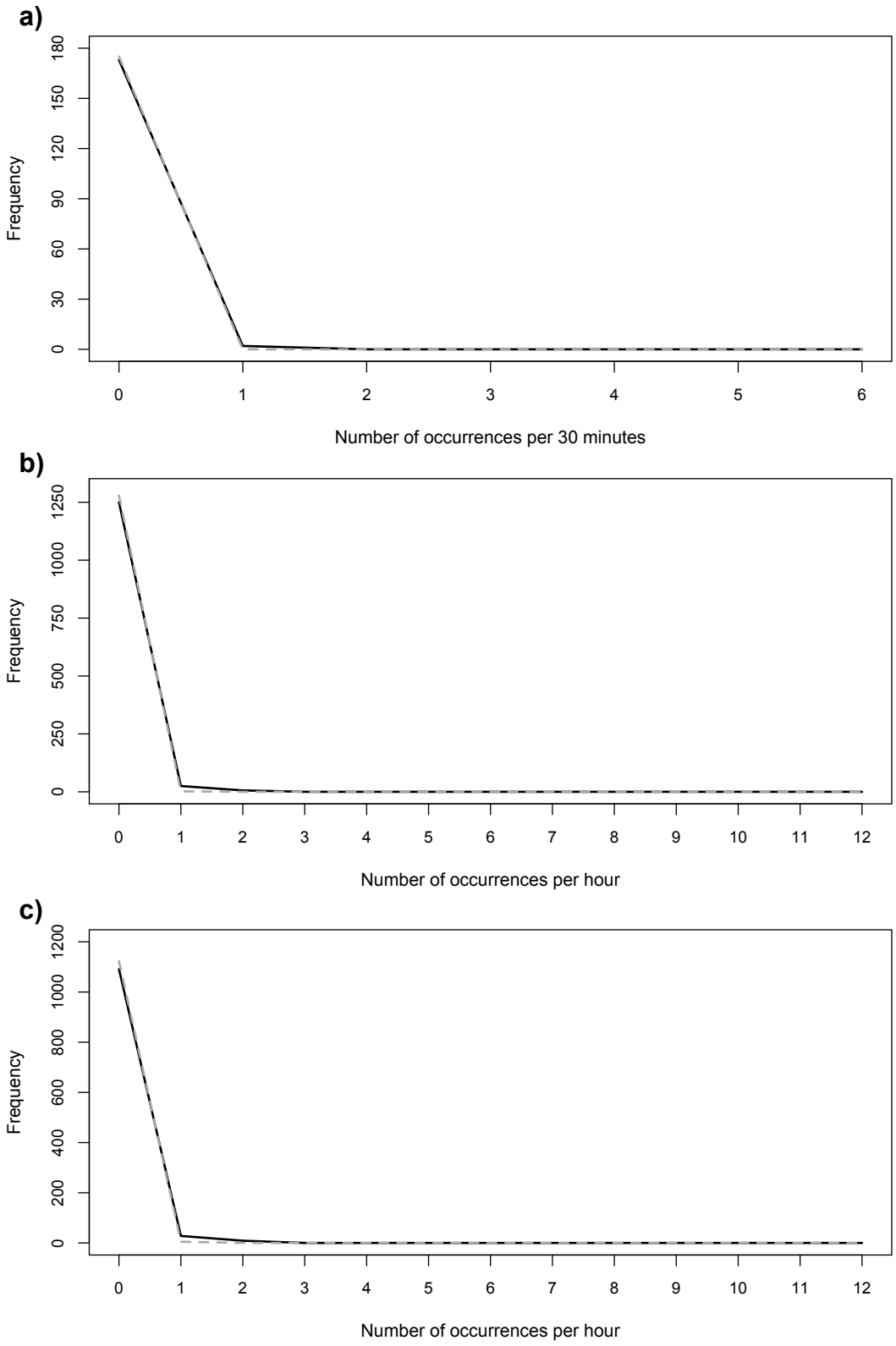


Figure A5.1: the predicted (dashed grey line) and the observed (solid black line) values for the pup check behavioural category for the **a)** 2007 (2007 & 2008 re-sighted individuals) **b)** 2008 and **c)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons. See Section 5.3.8 for more details on how these plots were constructed.

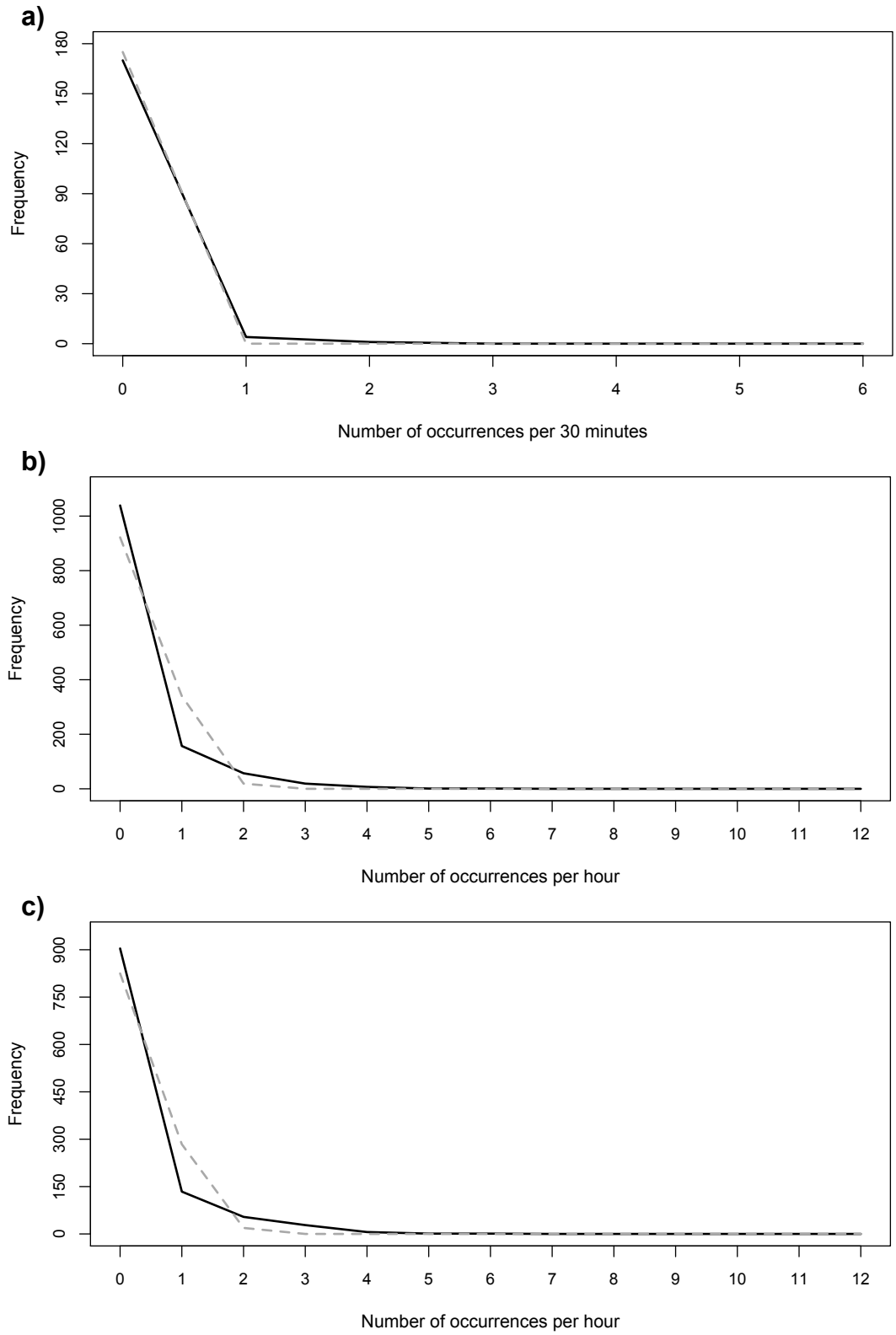


Figure A5.2: the predicted (dashed grey line) and the observed (solid black line) for the alert behavioural category for the **a)** 2007 (2007 & 2008 re-sighted individuals) **b)** 2008 and **c)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons. See Section 5.3.8 for more details on how these plots were constructed.

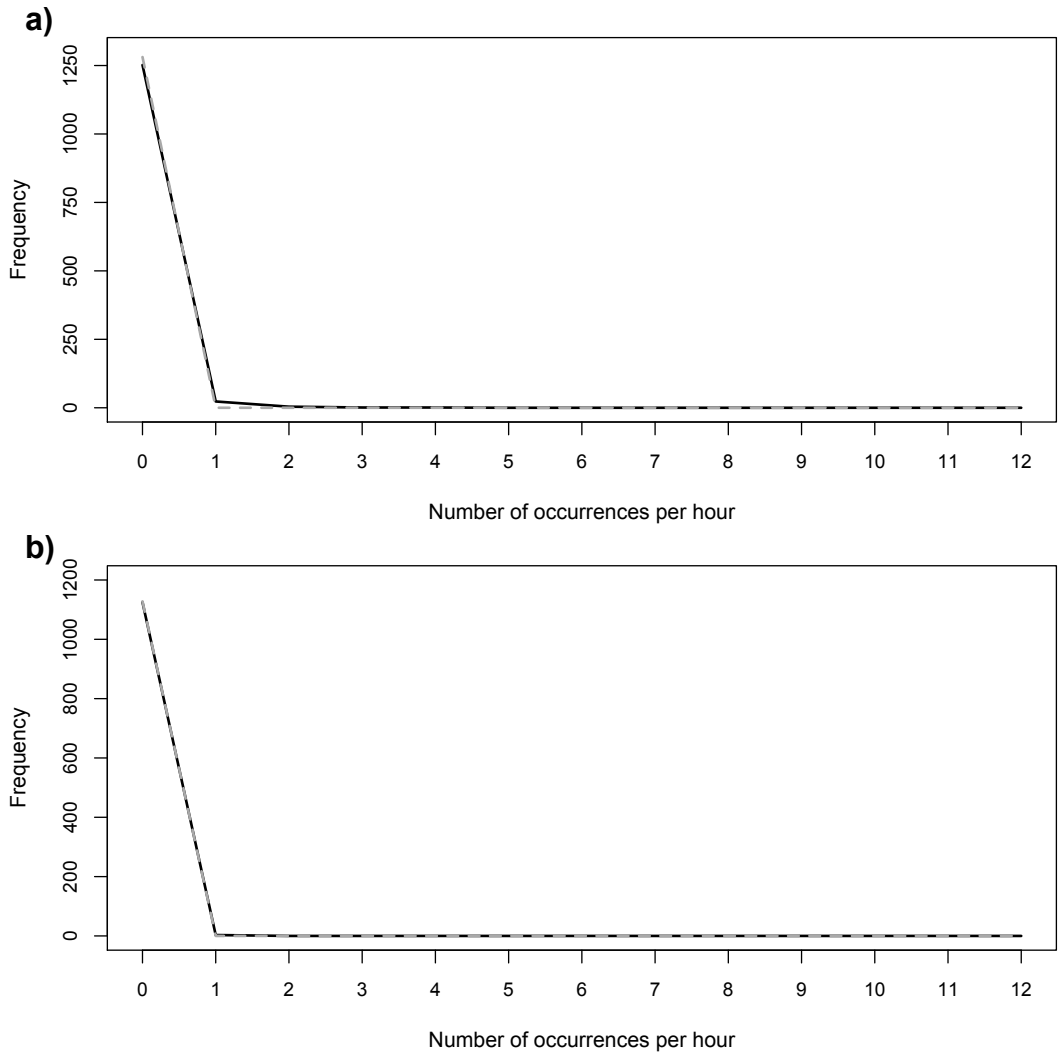


Figure A5.3: the predicted (dashed grey line) and the observed (solid black line) for the aggression behavioural category the **a)** 2008 and **b)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons. See Section 5.3.8 for more details on how these plots were constructed.

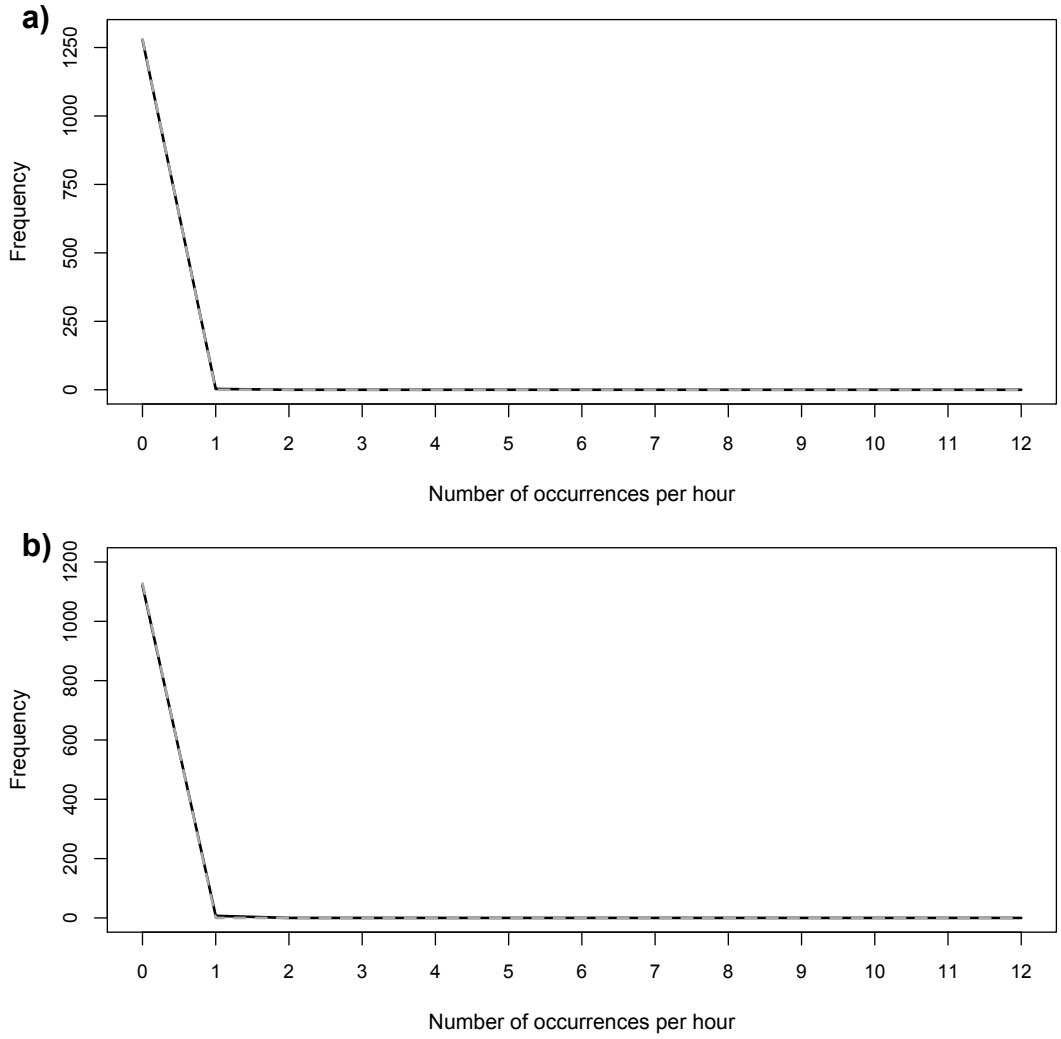


Figure A5.4: the predicted (dashed grey line) and the observed (solid black line) for the locomotion behavioural category the **a)** 2008 and **b)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons. See Section 5.3.8 for more details on how these plots were constructed.

Appendix: Chapter 6

Table A6.1: The number of models retained (from a possible 63) at each of the 5 stages of model selection (Section 6.4.2) for each of the pup check and the alert behavioural categories for each of the 4 analyses. Stage 1: models within a $\triangle < 6$; stage 2: after considering nested models; stage 3: redefining models after considering collinearity; stage 4: models within a $\triangle < 6$; stage 5: after considering nested models; see Chapter 5, Section 5.3.6 for a more detailed account of the model selection protocol. *Indicates that none of the models within the confidence set contained collinear covariates. Black cells indicate that there are no data for that particular analysis.

		Stage 1			Stage 2			Stage 3			Stage 4			Stage 5		
Behaviour	Years present	2007	2008	2009	2007	2008	2009	2007	2008	2009	2007	2008	2009	2007	2008	2009
Pup Check	2007 – 2009	26	31	18	1	2	4	1*	2*	4	1	2	2	1	2	2
	2007 & 2008	32	29		2	2		2*	2*		2	2		2	2	
	2008 & 2009		27	26		4	8		3	7		2	3		2	3
	2007 & 2009	28		32	1		7	1*		5	1		4	1		3
Alert	2007 – 2009	21	14	16	2	6	1	2*	6	1*	2	3	1	2	3	1
	2007 & 2008	18	10		3	6		3	6		3	2		2	2	
	2008 & 2009		16	16		8	1		7	2		4	2		3	1
	2007 & 2009	26		15	3		1	3		2	3		1	2		1

Table A6.2: The estimated dispersion parameters for the simplest models for the pup check and alert behavioural categories. Values greater than one indicate that the data are overdispersed (see Section 6.4.4). The simplest models for the pup check and alert behaviours are shown in Tables 6.1 and 6.2, respectively.

		Dispersion estimate		
Behaviour	Analyses	2007	2008	2009
Pup Check	2007 – 2009	0.824	1.077	0.970
	2007 & 2009	0.765	1.106	
	2008 & 2009		1.065	1.128
	2007 & 2009	0.821		0.968
Alert	2007 – 2009	1.137	1.463	1.188
	2007 & 2009	1.121	1.445	
	2008 & 2009		1.429	1.135
	2007 & 2009	1.142		1.230

Table A6.3: The ICC2 results for all possible combinations of the BLUPs extracted from the models retained in the confidence sets for the **pup check behavioural category** for individuals that were re-sighted in all three years (2007 - 2009; n = 8), 2007 & 2008 (n = 9), 2008 & 2009 (n = 15) and 2007 & 2009 (n = 9) (Table 6.1). The second column shows the combination of models, which begins with the most recent breeding season (e.g. for 2007 - 2009; the model numbers are arranged, 2009, 2008, 2007); the model numbers correspond to those shown in Table 6.1. Significant repeatability estimates are in bold.

Analyses	Model No.	ICC	F	*p*	lower	upper
2007 - 2009	1 + 1 + 1	0.019	1.1	0.44	-0.35	0.59
	1 + 2 + 1	0.03	1.1	0.42	-0.35	0.6
	2 + 1 + 1	0.13	1.4	0.29	-0.29	0.67
	2 + 2 + 1	0.14	1.4	0.27	-0.28	0.68
2007 & 2008	1 + 1	0	1.1	0.43	-0.77	0.66
	1 + 2	0	1	0.5	-0.77	0.66
	2 + 1	0.009	1	0.49	-0.76	0.66
	2 + 2	0.007	1	0.49	-0.76	0.66
2008 & 2009	**1 + 1**	**0.68**	**5**	**0.002**	**0.27**	**0.88**
	1 + 2	**0.69**	**5.2**	**0.002**	**0.29**	**0.89**
	2 + 1	**0.73**	**6**	**<0.001**	**0.35**	**0.9**
	2 + 2	**0.73**	**6.1**	**<0.001**	**0.36**	**0.9**
	3 + 1	**0.71**	**5.5**	**0.002**	**0.31**	**0.89**
	3 + 2	**0.71**	**5.6**	**0.001**	**0.32**	**0.89**
2007 & 2009	1 + 1	0	1	0.5	-0.77	0.66
	1 + 2	0.26	1.6	0.25	-0.55	0.78
	1 + 3	0.12	1.3	0.37	-0.67	0.72

Table A6.4: The ICC2 results for all possible combinations of the BLUPs extracted from the models retained in the confidence sets for the **alert behavioural category** for individuals that were re-sighted in all three years (2007 - 2009; n = 8), 2007 & 2008 (n = 9), 2008 & 2009 (n = 15) and 2007 & 2009 (n = 9) (Table 6.2). The second column shows the combination of models, which begins with the most recent breeding season (e.g. for 2007 - 2009; the model numbers are arranged, 2009, 2008, 2007); the model numbers correspond to those shown in Table 6.2. Significant repeatability estimates are in bold.

Analyses	Model No.	ICC	F	*p*	lower	upper
2007 - 2009	**1 + 1 + 1**	**0.58**	**4.6**	**0.007**	**0.12**	**0.88**
	1 + 2 + 1	**0.57**	**4.5**	**0.009**	**0.108**	**0.88**
	1 + 1 + 2	**0.64**	**5.6**	**0.003**	**0.2**	**0.9**
	1 + 2 + 2	**0.62**	**5.4**	**0.004**	**0.18**	**0.9**
	1 + 3 + 1	**0.57**	**4.5**	**0.008**	**0.11**	**0.88**
	1 + 3 + 2	**0.62**	**5.3**	**0.004**	**0.18**	**0.9**
2007 & 2008	**1 + 1**	**0.64**	**4.1**	**0.031**	**-0.043**	**0.91**
	1 + 2	**0.65**	**4.3**	**0.027**	**-0.015**	**0.91**
	2 + 1	**0.62**	**3.9**	**0.035**	**-0.07**	**0.9**
	2 + 2	**0.63**	**4.1**	**0.031**	**-0.046**	**0.91**
2008 & 2009	**1 + 1**	**0.7**	**5.4**	**0.002**	**0.3**	**0.89**
	1 + 2	**0.69**	**5.2**	**0.002**	**0.28**	**0.88**
	1 + 3	**0.68**	**5**	**0.002**	**0.27**	**0.88**
2007 & 2009	1 + 1	0.55	3.2	0.062	-0.192	0.88
	1 + 2	**0.66**	**4.5**	**0.025**	**0.004**	**0.91**

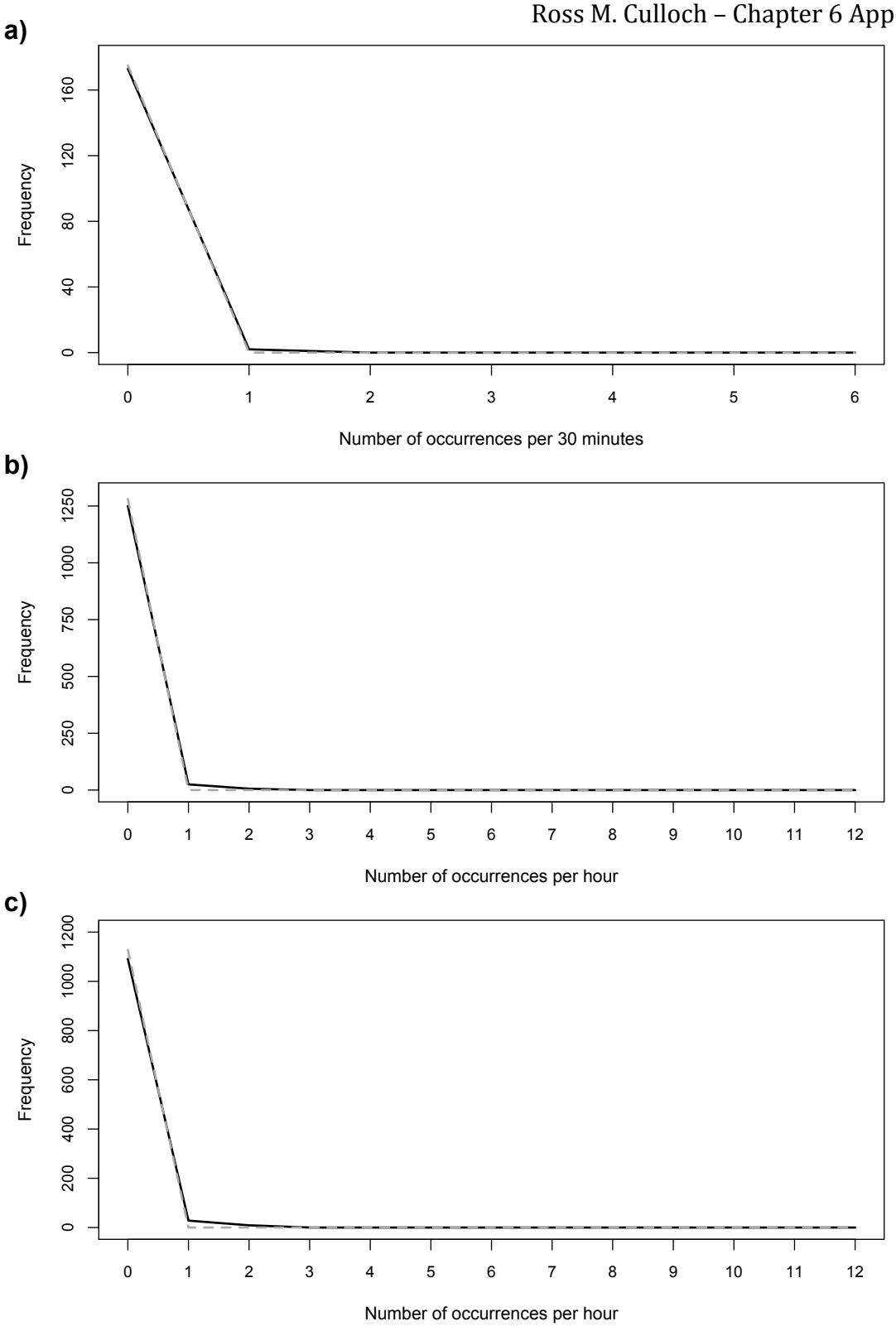


Figure A6.1: the predicted (dashed grey line) and the observed (solid black line) values for the pup check behavioural category for the **a)** 2007 (2007 & 2008 re-sighted individuals) **b)** 2008 and **c)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons. See Chapter 5, Section 5.3.8 for more details on how these plots were constructed. The plots for the breeding seasons were similar irrespective of which re-sighted individuals' dataset was used; therefore, only a subset of the goodness of fit plots is presented.

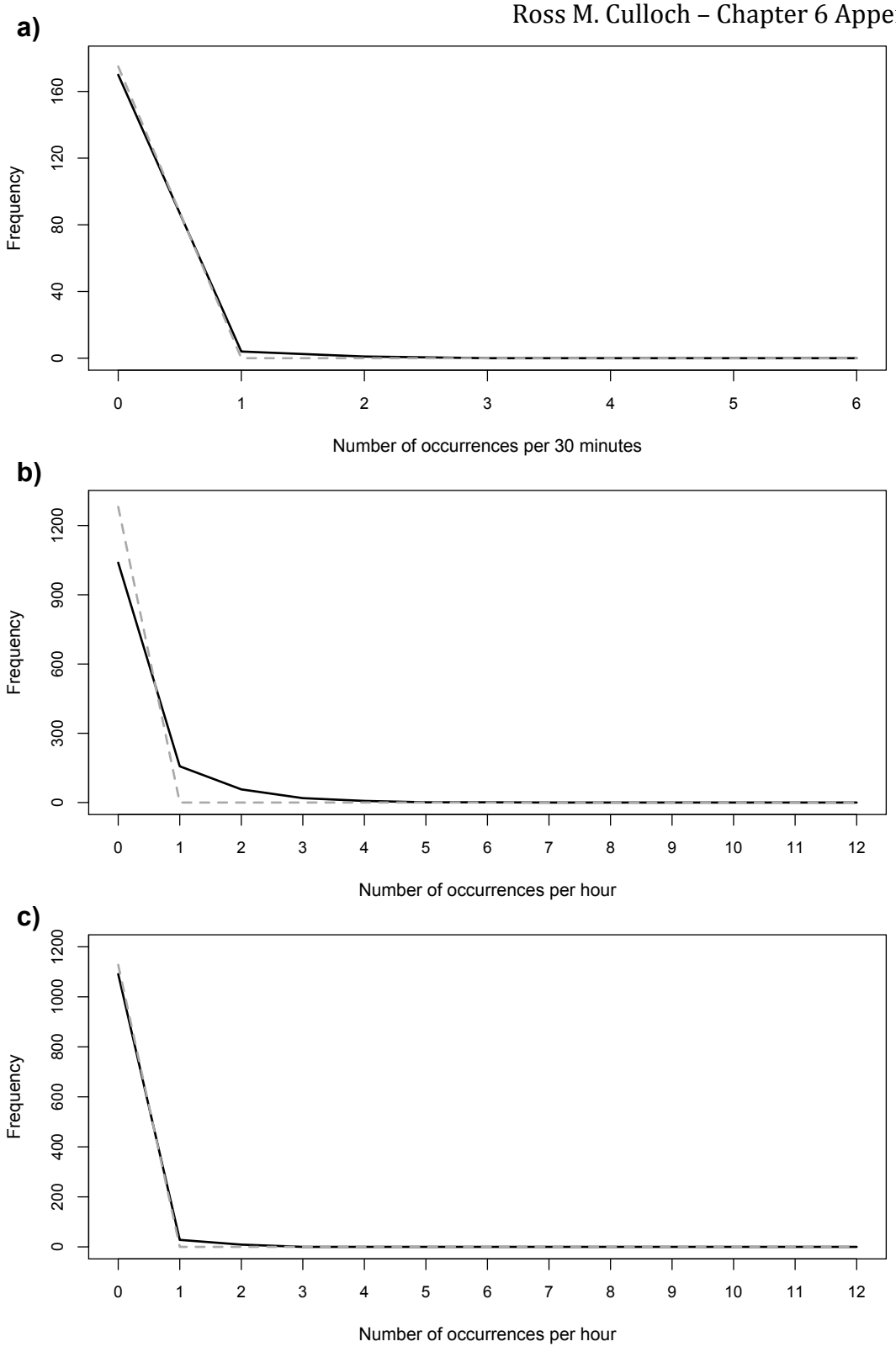


Figure A6.2: the predicted (dashed grey line) and the observed (solid black line) values for the alert behavioural category for the **a)** 2007 (2007 & 2008 re-sighted individuals) **b)** 2008 and **c)** 2009 (2008 & 2009 re-sighted individuals) breeding seasons. See Chapter 5, Section 5.3.8 for more details on how these plots were constructed. The plots for the breeding seasons were similar irrespective of which re-sighted individuals' dataset was used; therefore, only a subset of the goodness of fit plots is presented.

Chapter 7: Appendix

Section A

Quantitative comparisons and discussion of the behavioural and spatial data between the SA and the NSA

The comparative analyses are presented in Section 7.3.5, in the main chapter. The results showed that there was no significant difference between the pup check, alert or pup interactions behavioural categories between the two sites (Table A7.8 and Figure 7.1). For both breeding seasons, individuals in the NSA spent significantly more time in the comfort movement behavioural category, which is likely to be a result of the distance each observer was from the target individuals. Ross Culloch (RMC) was very close (min. distance = ca. 1 m; max. distance = ca. 80 m), which made it possible to record subtle comfort movements that may have been missed by Dr. Sean Twiss (SDT), who was considerably further away from the target individuals (min. distance = ca. 100 m; max. distance = ca. 500 m). In these scenarios, it is likely that SDT recorded the individual as resting, which may, in part explain the greater proportion of time spent resting by individuals within the SA. Following this supposition, if the resting and comfort movement behaviours are combined, then there is no significant difference between the NSA and the SA for the 2008 or the 2009 breeding seasons (Mann-Whitney U test: W = 320, p = 0.412; W = 268, p = 0.689, respectively).

Of the other behavioural categories, the proportion of time spent in: locomotion was significantly higher in the SA for both breeding seasons; presenting & nursing was significantly higher in the SA in 2008; aggression was significantly lower in the SA in 2008 (Table A7.8 and Figure 7.1). There is no reason to suspect that these significant differences were a result of the observers and/or their location in relation to the target individuals; however, they may be explained, in part, by the spatial data. In 2008, the distance between a mother and her nearest female neighbour was significantly shorter in the NSA than the SA (W = 142, p = 0.003; Table A7.9 and Figure 7.2). The median of the median for this covariate for the NSA in 2008 was 3.24 m (Table A7.9). Therefore, as mothers are known to become intolerant of conspecifics that approach within a range of ca. 3 - 4 m (Boness et al., 1982; Caudron, 1998; Pomeroy et al., 2000b), the closer proximity of neighbouring females in the NSA in 2008 may explain why these

females spent significantly more time being aggressive, than their counterparts in the SA (W = 410, p = 0.007; Table A7.8).

In both breeding seasons, females in the SA were generally closer to pools of water (Table A7.9 and Figure 7.2). Consequently, females in the SA may have been commuting shorter distances between pool and pup. This may be a result of the gradual decline in the numbers of pups being born on North Rona over the last decade (Chapter 2, Section 2.3); therefore, fewer seals on the colony has meant that access to water is not as heavily contested as it once was. A preliminary analysis of these data over the last 15 years does show that there has been a general downward trend in the distance between a female and her nearest pool (Figure A7.13). Although these are preliminary analyses, they do support the data presented here (the same general trend may also have occurred in the NSA; however, there are no maps of the NSA prior to 2007 to ascertain whether or not this is the case). Consequently, being in closer proximity to a pool would reduce the mothers' need to undertake long-distance commutes between pup and pool, which in turn reduces the likelihood of permanent mother-pup separation (Pomeroy et al., 1994; Redman et al., 2001).

If females undertook these short distance commutes more regularly, then this may explain why females in the SA spent significantly more time in the locomotion behavioural category (because locomotion was a more frequent event despite occurring for (presumably) shorter durations). Similarly, if females were returning to their pup more regularly in the SA, then this may also account for the generally higher proportion of time spent presenting & nursing; although it is important to note that a higher frequency does not necessarily mean longer durations. These hypotheses are based on limited quantitative evidence; however, as the mother-pup distances are not available, and without focal samples being collected in the SA to quantify the duration of the locomotion and the presenting & nursing behaviours, it is not possible to quantitatively address these suppositions. Nevertheless, if these were true, then this would be another indication that scan sampling may not be the best method for obtaining a representative sample of certain behaviours (in this instance, locomotion and presenting & nursing; Chapter 2, Section 2.5.4).

The collinearity of covariates

A brief summary of the collinearity analyses is presented in Section 7.3.7, in the main chapter. As expected, many of the continuous covariates were collinear with one another (Tables A7.10 - A7.18). Only three of the pairwise relationships were found to be collinear in all of the re-sighted individuals' datasets. These were density and nearest female neighbour (r min. = -0.63, r max. = -0.833, $p < 0.001$; n = 9), air temperature and pup age (r min. = -0.213, r max. = -0.505, $p < 0.001$; n = 9) and air temperature and rainfall (r min. = 0.085, r max. = 0.476, p min. < 0.001, p max. < 0.05; n = 6). The first of these correlations showed that the higher the density, the closer the mother is to her nearest female neighbour, which is unsurprising. The significant, negative relationship between the age of the pup and the air temperature is likely to be an effect of the seasonal changes in temperature and the peak of the breeding season, which occurs between 8th - 10th October (Hewer, 1959; Hiby et al., 1996; Twiss et al., 2000). Therefore, there are more pups being born in the earlier part of the breeding season when it is comparatively warmer. The positive relationship between the rainfall and the air temperature data was found in the NSA data (which used the same weather data as the SA); however, it was not consistently significant across all re-sighted individuals' datasets. As the SA data were fewer, the compliment of weather data used with the behavioural data was different between the two study sites. Nevertheless, the positive relationship between these two covariates for both study sites are explained by the occurrence of anticyclones, which are cold but dry, and depressions, which are relatively warm but wet. Therefore, this relationship (on a relatively coarse scale) is to be expected.

The relationships between the response and the explanatory variables

The relationships between the response variables and the continuous explanatory variables were tested using a Spearman's rank correlation coefficient (Zuur et al., 2009a). This was done for the nine re-sighted individuals' datasets, for the two behavioural categories, for all of the explanatory variables (including rainfall for the 2008 and 2009 re-sighted individuals' datasets; Tables A27 - A30). For the alert behavioural category, the activity of the pup had a positive

relationship across all re-sighted individuals' datasets. Furthermore, the pup age (positive relationship), air temperature (negative relationship) and pup age (negative relationship) also had a consistently significant relationship with the alert behavioural category in the 2008, 2009 and 2010 breeding seasons, respectively. For the pup check behaviour, with the exception of the 2008 datasets, the activity of the pup always had a significant, positive relationship. In the 2010 breeding season, density also had a consistently significant, positive relationship with this behaviour. However, no covariate was consistently significant with the pup check behavioural category in the 2008 breeding season.

The following three pages show the presence and absence data, collected by SDT, for individual postpartum female grey seals that were re-sighted in two or more breeding seasons within the SA. There were a total of 18 *actual* individuals (N = 18), which accounted for a total of 41 individuals over the three breeding seasons (n = 41; See Section 7.3.6). Each of the individuals (N = 18) that were re-sighted in the SA were given a prefix. These data are presented for each of the breeding seasons (**2008**, **2009** and **2010**) in tables **A7.1**, **A7.2** and **A7.3**, respectively. Day 1 in all three years is the 30th September. '1' indicates that the female was seen on that day; '0' indicates that the female was not seen on that day; the day the female gave birth is shown as a 'P' in a dark grey cell; P^ indicates that the pup was born on this day, but no behavioural data were collected; the day the female left the colony is shown as an 'L' in an dark gray cell; L* indicates that the leaving day is an estimate, which was based on the GIS and the observational data; grey cells are used to indicate that observational data were not collected for a particular individual on a given day (e.g. if the female was pregnant or if the female had left the colony); black cells are used to indicate days in which data were not collected for the entire day (i.e. SDT was involved in other fieldwork; see Section 7.3.1); the number of hours (to the nearest 30 minutes) that scan samples were carried out for a given day are noted in the tables (below the day number); the approximate total number of hours spent collecting scan samples for the 2008, 2009 and 2010 breeding seasons was 110, 143.5, 192, respectively. See table footnotes for additional information relating to specific individuals within each of the breeding seasons.

Table A7.1

Day/Number of hours per day observations were carried out

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
ID	-	-	-	-	-	-	-	-	*6.5*	*5.5*	-	*6.5*	*8.5*	*8*	*7.5*	-	*7.5*	-	*7*	*8*	-	*8*	*7.5*	-	*5.5*	*7.5*	-	-	*6.5*	-	*4.5*	*5.5*
992[1]							P^		1	1		1	1	1	1		1		1	1		1	1		1	1			L			
994																						P^	0		1	1			1		1	1y
995				P^					1	1		1	1	1	1		1		1	1		1	1		1	L						
996							P^		1	1		1	1	1	1		0		0	0		0	0		0	0			0		0	0
998	P^								1	1		1	1	1	1		1		1	L												
999									P^	0		1	1	1	1		1		1	1		1	1		1	1		L*				
9910						P^			1	1		1	1	1	1		1		1	1		1	1		1	1	L*					
9912													P^	0	0		1		1	1		1	1		1	1			1		1	1y
9914																					P^	0	0		1	1			1		1	1y
9915													P^	0	0		1		1	1		1	1		1	1			1		1	1x
9923								P^	0	0		1	1	1	1		1		1	1		1	1		1	1		L*				
9924						P^			0	0		1	1	1	1		1		1	1		1	1	L*								

992[1]: pup date of birth is an estimate; 1x: mother was last mapped on day 31; 1y: mother was still on the colony on day 33

Table A7.2

Day/Number of hours per day observations were carried out

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
ID	-	-	*6.5*	-	*8*	*5*	-	*9*	*5.5*	*6.5*	-	*8.5*	-	*8*	*3.5*	*7*	-	*8.5*	*4*	-	*8.5*	*4*	-	*8*	*5*	-	*7.5*	*4*	*8*	-	*7.5*	*3*	*8*
991[1]			0		1	1		1	1	1		1		1	L*																		
994																								P^	0		1	1	1		1	1	1z
995		P^	1		1	1		1	1	1		1		1	1	1		1	1		1	1	L*										
9910					P^	0		1	1	1		1		1	1	1		1	1		1	1		1	1	L*							
9912								P^	0	0		1		1	1	1		1	1		1	1		1	1		1	1	1		1	L*	
9914																							P	1	1		1	1	1		1	1	1z
9915											P^	0		1	1	1		1	1		1	1		1	1		1	1	1		1	1	1x
9923[1]					P^	0		0	1	1		1		1	1	1		1	1	L*													
9924[1]																		P^	0		1	1		1	1		1	1	1		1	1	1y
9929						P^		1	1	1		1		1	1	1		1	1		1	1		L*									
9930						P^		1	1	1		1		1	1	1		1	1		1	1		1	1	L*							
9932									P^	0		1		1	1	1		1	1		1	1		1	1		1	1	1		L*		
9939									P^	0		1		1	1	1		1	1		1	1		1	1		1	1	L*				
9942											P^	0		1	1	1		1	1		1	1		1	1		1	1	L*				
9945															P^	0		0	0		0	0		1	1		1	1	1		1	1	1y

991[1]: pup date of birth was the 28th September; 9923[1]: pup date of birth is an estimate; 9924[1]: pup date of birth is an estimate; 1x: mother was last mapped on day 32; 1y: mother was last mapped on day 33; 1z: mother was still on the colony on day 34

Table A7.3

Day/Number of hours per day observations were carried out

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
	4	*10.5*	*10*	*10*	*-*	*10*	*-*	*10*	*4*	*10*	*-*	*10*	*5*	*-*	*10*	*5*	*-*	*10*	*4.5*	*9.5*	*-*	*9.5*	*9.5*	*-*	*9.5*	*6*	*3.5*	*-*	*7.5*	*4.5*	*7.5*	*8*	*-*	*4*
991[1]	1	1	1	1		1		1	1	1		1	1	L*																				
992									P^	0		1	1		1	1		1	1	1		1	1		1	1	1		1	0	1	L*		
995					P^	1		1	1	1		1	1		1	1		1	1	1		1	1		1	1	1		1	L				
996				P^		1		1	1	1		1	1		1	1		1	1	1		1	1		1	1	L*							
998[1]	1	1	1	1		1		1	1	1		1	1		1	1		1	L*														
999									P^	0		1	1		1	1		1	1	1		1	1		1	1	1		1	L*				
9910				P^		0		1	1	1		1	1		1	1		1	1	1		1	1	L										
9912							P^	0	1	1		1	1		1	1		1	1	1		L												
9914																					P^	0	0		1	1	1		1	1	1	1		1y
9915																				P^		1	1		1	1	1		1	1	1	1		1y
9929									P^	0		1	1		1	1		1	1	1		1	1		1	1	1	L*						
9930						P^		0	0	0		1	1		1	1		1	1	1		1	1		1	1	1		1	1	L*			
9932				P^		1		1	1	1		1	1		1	1		1	1	1		1	1	L*										
9939[1]									P^	0		0	0		0	0		0	0	0		0	0		1	1	1		1	1	1	1		1x
9942										P^		1	1		1	1		1	1	1		1	1		1	1	1		L					
9945										P^		0	0		1	1		1	1	1		1	1		1	1	1		1	L*				

991[1]: pup date of birth was the 25th September; 998[1]: pup date of birth was the 25th September; 9939[1]: pup date of birth is an estimate; 1x: mother was last mapped on day 33; 1y: mother was still on the colony on day 35

Table A7.4: The non-parametric summary statistics for the gross proportion of time spent in each of the nine behavioural categories (including the sex behavioural category) for the postpartum females (n = 70) for all three years (2008 - 2010) combined. Summary statistics for the proportion of time spent out-of-sight and for the number of scan samples per individual are given in the penultimate and last row, respectively.

Behaviour	Median	IQR	Min.	Max.
Resting	80.98	4.88	66.94	94.22
Comfort Move	1.7	1.21	0.27	4.16
Pup Check	1.87	1.07	0.65	4.1
Alert	5.69	2.66	1.28	11.83
Locomotion	0.99	0.63	0.24	2.42
Presenting & Nursing	5.03	1.99	0	10.72
Pup Interactions	1.63	1.25	0	4.23
Aggression	0.59	0.54	0	1.65
Sex	0	0.55	0	2.25
Out-Of-Sight*	0	0.18	0.93	33.96
Scan Samples	***852***	***411***	***346***	***1418***

*Note that the data for the nine behavioural categories displayed here were calculated without out-of-sight. The summary data presented for out-of-sight was calculated in a separate analysis.

Table A7.5: The distance (m) between a female's pupping sites between breeding seasons; ID is the individuals' unique identification code; the age of the pup with respect to the pupping site location was variable; * indicates that for at least one of the breeding seasons the females' pups was > 3 days old (see Table A7.6 for more details). A grey cell indicates that the individual was not seen in one of the two breeding seasons.

	Breeding seasons		
ID	2008 & 2009	2009 & 2010	2008 & 2010
992*			16.47
994	17.62		
995*	12.66	22.88	20.95
996			45.71
998*			19.98
999*			79.69
9910	28.66	25.04	16.76
9912	17.13	51.98	46.42
9914	20.48	41.64	60.81
9915	58.14	23.20	38.92
9923	60.58		
9924*	44.05		
9929*		51.39	
9930*		50.99	
9932		35.05	
9939*		37.28	
9942		86.84	
9945*		79.92	

Table A7.6: The age of the pup when the mother was first mapped postpartum (i.e. the location used to define the pupping site location) and the number of locations for each of the individuals for each of the three breeding seasons (n); ID is the individuals' unique identification code. A grey cell indicates that the individual was not seen in that breeding season.

	Breeding season					
	2008		2009		2010	
ID	Pup age	n	Pup age	n	Pup age	n
992	4	6			2	13
994	2	5	3	4		
995	4	11	1	12	1	16
996	1	5			1	13
998	8	8			5	13
999	2	11			2	13
9910	2	8	3	7	3	10
9912	3	10	3	14	1	8
9914	3	5	1	7	3	8
9915	3	9	2	13	1	10
9923	3	11	3	6		
9924	5	6	2	8		
9929			1	7	12	3
9930			1	5	15	4
9931			2	7	1	4
9932			2	12	1	12
9939			4	5	11	7
9942			2	8	1	12
9945			8	7	4	11

Table A7.7: The non-parametric summary statistics for the gross spatial data for the postpartum females (n = 64) for all three years (2008 - 2010) combined.

Spatial Variable	Median	IQR	Min.	Max.
Density (10 m buffer)	3	3	0	13
Nearest Female (m)	4.81	4.38	1.27	76.93
Distance to pool (m)	2.2	2.95	0	38.89

Table A7.8: The results of the Mann-Whitney U tests for the comparisons between the median proportion of time spent in each behavioural category for individuals in the SA and the NSA during the 2008 (n = 20, n = 28, respectively) and 2009 (n = 23, n = 30, respectively) breeding seasons. All significant results are in bold. See the footnote for the behavioural codes.

		R	CM	PC	A	L	MP	PINT	AGG
2008	*p*	0.055	**<0.001**	0.541	0.565	**<0.001**	**0.004**	0.198	**0.007**
	W	188	**552**	310	308	**111**	**145**	218	**410**
2009	*p*	**0.019**	**<0.001**	0.965	0.155	**0.010**	0.087	0.810	0.080
	W	**215**	**675**	342	425	**203**	249	359	443

R = Resting; CM = Comfort Movement; PC = Pup Check; A = Alert; L = Locomotion; MP = Presenting & Nursing; PINT = Pup Interactions; AGG = Aggression

Table A7.9: The results of the Mann-Whitney U tests for the comparisons between the spatial data from the SA and the NSA. The tests compared the median value for each of the individuals in the SA and the NSA during the 2008 (n = 20, n = 28, respectively) and 2009 (n = 23, n = 30, respectively) breeding seasons. All significant results are in bold.

		Density	Nearest female	Distance to pool
2008	*p*	0.412	**0.003**	0.356
	W	319	**142**	325
2009	*p*	0.281	0.135	**0.002**
	W	285.5	429	**515**

The following 5 pages show:

Tables A7.10 - A7.18: The collinearity analyses for the nine re-sighted individuals' datasets (2008 - 2010; 2008 & 2009; 2009 & 2010; 2008 & 2010). The analyses were done using the Spearman's rank correlation coefficient. The *p* value is shown above and the r value is shown below. Significant results are in bold. The covariates are: the proportion of time the pup spent active (ACT); the density of females within a 10 m buffer zone of the target female (DEN); the distance between a mother and her nearest pool (POOL); the amount of rainfall (RAIN); the air temperature (TEMP); the age of the pup (AGE); the nearest female neighbour (NFN). A grey cell indicates that there is no data available for the covariate. See Section 7.3.7 for more details on each of the covariates.

Table A7.10: The collinearity analyses for the 2008 re-sighted individuals' dataset for the females that were re-sighted in all three years (2008 - 2010) (n = 5).

	ACT	DEN	POOL	RAIN	TEMP	AGE	NFN
ACT	-	0.465	**0.006**	0.59	0.07	0.567	0.511
	-	-0.041	**0.152**	0.03	-0.101	-0.032	0.037
DEN		-	0.22	**0.023**	0.399	**0.014**	**<0.001**
		-	0.068	**-0.127**	-0.047	**-0.137**	**-0.833**
POOL			-	**0.002**	**<0.001**	0.26	**<0.001**
			-	**-0.174**	**-0.446**	0.063	**-0.265**
RAIN				-	**<0.001**	0.96	**0.025**
				-	**0.202**	-0.003	**0.125**
TEMP					-	**<0.001**	**0.001**
					-	**-0.502**	**0.178**
AGE						-	0.473
						-	-0.04
NFN							-
							-

Table A7.11: The collinearity analyses for the 2009 re-sighted individuals' dataset for the females that were re-sighted in all three years (2008 - 2010) (n = 5).

	ACT	DEN	POOL	RAIN	TEMP	AGE	NFN
ACT	-	**<0.001**	0.96	0.293	0.542	**<0.001**	**0.002**
	-	**-0.19**	0.003	0.054	0.032	**-0.176**	**0.159**
DEN		-	0.16	0.794	**0.005**	**<0.001**	**<0.001**
		-	0.073	-0.014	**0.145**	**0.25**	**-0.675**
POOL			-	0.829	0.194	**<0.001**	**<0.001**
			-	0.011	-0.067	**0.305**	**0.18**
RAIN				-	**<0.001**	0.299	0.307
				-	**0.443**	0.054	0.053
TEMP					-	**<0.001**	**<0.001**
					-	**-0.219**	**-0.192**
AGE						-	**0.022**
						-	**-0.118**
NFN							-
							-

Table A7.12: The collinearity analyses for the 2010 re-sighted individuals' dataset for the females that were re-sighted in all three years (2008 - 2010) (n = 5).

	ACT	DEN	POOL	RAIN	TEMP	AGE	NFN
ACT	- -	0.329 -0.05	0.507 0.034		0.982 0.001	0.926 0.005	0.801 0.013
DEN		- -	0.145 -0.075		**<0.001** **0.188**	**<0.001** **-0.307**	**<0.001** **-0.779**
POOL			- -		0.578 0.029	**<0.001** **0.208**	0.505 0.034
RAIN				- -			
TEMP					- -	**<0.001** **-0.303**	**0.005** **-0.143**
AGE						- -	**<0.001** **0.294**
NFN							- -

Table A7.13: The collinearity analyses for the 2008 re-sighted individuals' dataset for the females that were re-sighted in 2008 & 2009 (n = 8).

	ACT	DEN	POOL	RAIN	TEMP	AGE	NFN
ACT	- -	0.089 -0.076	**0.036** **0.094**	0.506 0.03	**0.029** **-0.1**	0.967 0.002	0.231 0.054
DEN		- -	0.35 0.042	0.18 -0.06	**0.005** **0.127**	**<0.001** **-0.201**	**<0.001** **-0.735**
POOL			- -	0.756 -0.014	**<0.001** **-0.375**	**0.004** **0.129**	**<0.001** **-0.173**
RAIN				- -	**<0.001** **0.173**	0.683 0.018	**0.018** **0.106**
TEMP					- -	**<0.001** **-0.505**	0.514 -0.029
AGE						- -	**0.047** **0.089**
NFN							- -

Table A7.14: The collinearity analyses for the 2009 re-sighted individuals' dataset for the females that were re-sighted in 2008 & 2009 (n = 8).

	ACT	DEN	POOL	RAIN	TEMP	AGE	NFN
ACT	-	**<0.001**	0.748	0.1	0.384	**<0.001**	**<0.018**
	-	**-0.166**	-0.014	0.074	0.039	**-0.172**	**0.105**
DEN		-	0.126	0.805	**<0.001**	**<0.001**	**<0.001**
		-	0.068	-0.011	**0.176**	**0.166**	**-0.63**
POOL			-	0.339	0.251	**<0.001**	0.192
			-	-0.043	-0.051	**0.342**	0.058
RAIN				-	**<0.001**	0.667	**0.04**
				-	**0.47**	0.019	**0.092**
TEMP					-	**<0.001**	0.005
					-	**-0.213**	-0.124
AGE						-	0.587
						-	-0.024
NFN							-
							-

Table A7.15: The collinearity analyses for the 2009 re-sighted individuals' dataset for the females that were re-sighted in 2009 & 2010 (n = 11).

	ACT	DEN	POOL	RAIN	TEMP	AGE	NFN
ACT	-	<0.001	0.408	0.145	**0.022**	**<0.001**	**<0.001**
	-	-0.153	0.032	0.055	**0.087**	**-0.195**	**0.154**
DEN		-	**<0.001**	0.81	0.156	**<0.001**	**<0.001**
		-	**-0.185**	0.009	0.054	**0.258**	**-0.7**
POOL			-	**0.002**	**0.005**	0.114	**<0.001**
			-	**0.12**	**0.106**	0.06	**0.235**
RAIN				-	**<0.001**	**<0.001**	0.708
				-	**0.476**	**0.127**	-0.014
TEMP					-	**<0.001**	0.076
					-	**-0.301**	-0.067
AGE						-	**<0.001**
						-	**-0.198**
NFN							-
							-

Table A7.16: The collinearity analyses for the 2010 re-sighted individuals' dataset for the females that were re-sighted in 2009 & 2010 (n = 11).

	ACT	DEN	POOL	RAIN	TEMP	AGE	NFN
ACT	-	0.834	0.242		**0.002**	**0.034**	0.303
	-	0.008	-0.043		**0.113**	**-0.077**	-0.037
DEN		-	**<0.001**		0.736	0.881	**<0.001**
		-	**-0.12**		0.012	0.005	**-0.756**
POOL			-		**0.012**	**<0.001**	**<0.001**
			-		**-0.091**	**0.179**	**0.185**
RAIN				-			
				-			
TEMP					-	**<0.001**	0.37
					-	**-0.486**	0.033
AGE						-	**0.014**
						-	**0.089**
NFN							-
							-

Table A7.17: The collinearity analyses for the 2008 re-sighted individuals' dataset for the females that were re-sighted in 2008 & 2010 (n = 9).

	ACT	DEN	POOL	RAIN	TEMP	AGE	NFN
ACT	-	0.591	0.229	0.793	0.442	0.212	0.564
	-	-0.023	0.051	-0.011	-0.033	-0.053	-0.025
DEN		-	**<0.001**	**0.002**	0.378	0.181	**<0.001**
		-	**-0.324**	**-0.129**	-0.038	0.057	**-0.822**
POOL			-	0.642	**<0.001**	0.696	**<0.001**
			-	-0.02	**-0.221**	-0.017	**0.172**
RAIN				-	**0.046**	0.095	**0.027**
				-	**0.085**	0.071	**0.094**
TEMP					-	**<0.001**	**<0.001**
					-	**-0.482**	**0.159**
AGE						-	**0.031**
						-	**-0.092**
NFN							-
							-

Table A7.18: The collinearity analyses for the 2010 re-sighted individuals' dataset for the females that were re-sighted in 2008 & 2010 (n = 9).

	ACT	DEN	POOL	RAIN	TEMP	AGE	NFN
ACT	- -	0.88 0.005	0.381 -0.032		0.718 0.013	0.315 -0.036	0.283 -0.039
DEN		- -	**<0.001** **0.165**		**<0.001** **0.158**	0.245 -0.042	**<0.001** **-0.746**
POOL			- -		**<0.001** **0.191**	**<0.001** **0.19**	**0.002** **-0.111**
RAIN				- -			
TEMP					- -	**<0.001** **-0.377**	0.088 -0.062
AGE						- -	0.808 0.009
NFN							- -

Table A7.19: The summary of the results for the 'best' distribution for each of the re-sighted individuals' datasets for the pup check and alert behavioural categories for individuals re-sighted in: all 3 years (2008 - 2010; n = 5), 2008 & 2009 (n = 8), 2009 & 2010 (n = 11) and 2008 & 2010 (n = 9). The table shows the distributions used (BB: beta-binomial (2 d.f.); B: binomial (1 d.f.)); the models are ranked by their △ value. The BB distribution is in bold.

	2008 - 2010						**2008 & 2009**				**2009 & 2010**				**2008 & 2010**			
	2008		**2009**		**2010**		**2008**		**2009**		**2009**		**2010**		**2008**		**2010**	
Behaviour	**Dist.**	△	**Dist.**	△	**Dist.**	△	**Dist.**	△	**Dist.**	△	**Dist.**	△	**Dist.**	△	**Dist.**	△	**Dist.**	△
Pup	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**
Check	B	6.5	B	6.7	B	1.4	B	7.4	B	10.1	B	3.9	B	7.5	B	13.7	B	9.8
Alert	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**	**BB**	**0**
	B	6.1	B	36.9	B	29.5	B	12.4	B	43.2	B	66.7	B	65.1	B	42.6	B	69.4

Table A7.20: The difference between the AICc for the global model and the 'best' model using the beta-binomial (BB) and the binomial (B) distribution. The BB was used to define the 'best' model and the B distribution was applied to the same model to ascertain if the additional binomial variance was required (see Chapter 5, Appendix, Section A). Results in bold italics indicate that the B distribution was the 'better' of the two; the converse is true for the standard text. Black cells indicate that there are no data for that particular analysis (for example, 2009 is omitted from the analysis of those individuals that were re-sighted in 2008 & 2010, only).

	Years					
	2008		2009		2010	
Behaviour	Full	Best	Full	Best	Full	Best
Alert	***0.027***	1.093	17.387	18.328	6.906	8.877
Pup Check	***0.143***	2.945	0.34	10.297	***2.361***	***2.027***
Alert	2.42	6.23	16.166	18.254		
Pup Check	***0.12***	2.785	1.916	3.728		
Alert			33.396	44.381	22.839	25.461
Pup Check			***0.8***	11.286	***2.026***	2.453
Alert	5.007	4.842			26.158	28.704
Pup Check	***0.875***	9.258			1.229	4.905

Table A7.21: The estimated dispersion parameters for the simplest models for the pup check and alert behavioural categories. Values greater than one indicate that the data are overdispersed (see Section 7.3.8). The simplest models for the pup check and alert behaviours are shown in Tables 7.4 and 7.6, respectively.

		Dispersion estimate		
Behaviour	Analyses	2008	2009	2010
Pup Check	2008 - 2010	1.137	1.021	1.126
	2008 & 2009	1.092	1.050	
	2009 & 2010		0.969	1.148
	2008 & 2010	1.234		1.185
Alert	2008 - 2010	1.236	1.279	1.140
	2008 & 2009	1.254	1.245	
	2009 & 2010		1.334	1.200
	2008 & 2010	1.213		1.255

Table A7.22: ICC3 analyses for all 3 years (2008 - 2010; n = 5), 2008 & 2009 (n = 8), 2009 & 2010 (n = 11), 2008 & 2010 (n = 9). All significant results are in bold. Where ICC values are negative the best estimate for repeatability is zero (Hayes & Jenkins, 1997; Bell et al., 2009). The lower and upper columns show the 95% confidence limits.

Behaviour	Years	ICC	F	*p*	lower	upper
Resting	**2008 – 2010**	**0.69**	**7.6**	**0.008**	**0.14**	**0.96**
	2008 & 2009	0.35	2.1	0.18	-0.41	0.82
	2009 & 2010	**0.51**	**3.1**	**0.038**	**-0.063**	**0.83**
	2008 & 2010	0.54	3.3	0.054	-0.14	0.87
Comfort Movement	2008 – 2010	-0.13	0.65	0.65	-0.41	0.62
	2008 & 2009	**0.59**	**3.9**	**0.047**	**-0.12**	**0.9**
	2009 & 2010	-0.18	0.69	0.73	-0.67	0.41
	2008 & 2010	-0.25	0.6	0.76	-0.76	0.45
Pup Check	2008 – 2010	-0.31	0.29	0.87	-0.46	0.35
	2008 & 2009	**0.8**	**9.1**	**0.005**	**0.29**	**0.96**
	2009 & 2010	-0.51	0.33	0.96	-0.83	0.066
	2008 & 2010	0.131	1.3	0.36	-0.55	0.7
Alert	**2008 – 2010**	**0.64**	**6.2**	**0.014**	**0.073**	**0.95**
	2008 & 2009	0.35	2.1	0.18	-0.41	0.82
	2009 & 2010	**0.61**	**4.2**	**0.013**	**0.093**	**0.87**
	2008 & 2010	**0.78**	**8.2**	**0.004**	**0.3**	**0.95**
Locomotion	2008 – 2010	-0.16	0.58	0.68	-0.42	0.58
	2008 & 2009	0.31	1.9	0.21	-0.45	0.81
	2009 & 2010	0.21	1.5	0.24	-0.39	0.68
	2008 & 2010	-0.24	0.62	0.74	-0.76	0.46
Presenting & Nursing	2008 – 2010	0.48	3.8	0.051	-0.091	0.92
	2008 & 2009	0.014	1	0.49	-0.66	0.67
	2009 & 2010	0.29	1.8	0.17	-0.31	0.73
	2008 & 2010	0.34	2.1	0.16	-0.37	0.8
Pup Interaction	**2008 – 2010**	**0.53**	**4.4**	**0.037**	**-0.048**	**0.93**
	2008 & 2009	**0.65**	**4.7**	**0.029**	**-0.032**	**0.92**
	2009 & 2010	**0.49**	**2.9**	**0.046**	**-0.091**	**0.82**
	2008 & 2010	0.41	2.4	0.12	-0.3	0.83
Aggression	2008 – 2010	0.214	1.8	0.22	-0.27	0.84
	2008 & 2009	0.56	3.5	0.059	-0.17	0.89
	2009 & 2010	0.105	1.2	0.37	-0.48	0.62
	2008 & 2010	0.1	1.22	0.39	-0.57	0.69

Table A7.23: The number of models retained (from a possible 127) at each of the 5 stages of model selection for the pup check and alert behavioural categories for each of the 4 analyses. Stage 1: models within a △ < 6; stage 2: after considering nested models; stage 3: redefining models after considering collinearity; stage 4: models within a △ < 6; stage 5: after considering nested models; see Section 7.3.8 for a more detailed account of the model selection protocol. *Indicates that none of the models within the confidence set contained collinear covariates. Grey cells indicate that there are no data for that particular analysis.

		Stage 1			Stage 2			Stage 3			Stage 4			Stage 5		
Behaviour	Years	2008	2009	2010	2008	2009	2010	2008	2009	2010	2008	2009	2010	2008	2009	2010
Pup Check	2008 – 2010	29	52	30	1	1	4	1*	1*	7	1	1	2	1	1	2
	2008 & 2009	36	72		7	6		13	9		6	8		5	5	
	2009 & 2010		26	17		1	5		1*	13		1	2		1	2
	2008 & 2010	56		17	2		2	5		5	3		3	2		2
Alert	2008 – 2010	29	14	30	6	4	4	13	9	8	5	2	4	3	1	3
	2008 & 2009	20	13		8	3		15	9		2	2		2	1	
	2009 & 2010		16	22		6	2		13	5		2	1		2	1
	2008 & 2010	17		30	2		3	7		9	1		4	1		2

Table A7.24: The number of models retained (from a possible 63) at each of the 5 stages of model selection for each of the pup check and the alert behavioural categories for each of the 4 analyses. Stage 1: models within a △ < 6; stage 2: after considering nested models; stage 3: redefining models after considering collinearity; stage 4: models within a △ < 6; stage 5: after considering nested models; see Section 7.3.8 for a more detailed account of the model selection protocol. *Indicates that none of the models within the confidence set contained collinear covariates. Grey cells indicate that there are no data for that particular analysis.

		Stage 1			Stage 2			Stage 3			Stage 4			Stage 5		
Behaviour	Years	2008	2009	2010	2008	2009	2010	2008	2009	2010	2008	2009	2010	2008	2009	2010
Pup Check	2008 – 2010	32	26	16	2	1	3	3	1*	3	2	1	1	1	1	1
	2008 & 2009	20	32		4	4		4*	4		4	3		4	3	
	2009 & 2010		30	14		1	5		1*	6		1	1		1	1
	2008 & 2010	30		16	1		5	1*		5	1		3	1		2
Alert	2008 – 2010	16	10	30	7	4	3	7	4	3*	2	2	3	2	1	3
	2008 & 2009	11	8		3	2		4	4		2	2		2	1	
	2009 & 2010		6	28		3	3		5	4		2	3		2	1
	2008 & 2010	15		25	1		2	1*		2*	1		2	1		2

Table A7.25: The ICC2 results for all possible combinations of the BLUPs extracted from the models retained in the confidence sets for the **pup check behavioural category** for individuals that were re-sighted in all three years (2008 - 2010; n = 5), 2008 & 2009 (n = 8), 2009 & 2010 (n = 11) and 2008 & 2010 (n = 9) (Table 7.4). The second column shows the combination of models, which begins with the most recent breeding season (e.g. for 2008 - 2010; the model numbers are arranged, 2010, 2009, 2008); the model numbers correspond to those shown in Table 7.4. Significant repeatability estimates are in bold.

Analyses	Model No.	ICC	F	p	upper	lower
2010/2009/2008	1 & 1 & 1	-0.23	0.55	0.71	-0.59	0.62
2009/2008	1 & 1	0.43	2.3	0.142	-0.43	0.86
	1 & 2	**0.63**	**4**	**0.043**	**-0.125**	**0.92**
	1 & 3	**0.83**	**9.5**	**0.004**	**0.34**	**0.96**
	1 & 4	**0.41**	**2.2**	**0.016**	**-0.46**	**0.85**
	2 & 1	0.4	2.2	0.16	-0.47	0.85
	2 & 2	0.55	3.1	0.07	-0.27	0.89
	2 & 3	**0.78**	**7.2**	**0.009**	**0.18**	**0.95**
	2 & 4	0.37	2	0.18	-0.51	0.84
	3 & 1	0.41	2.2	0.16	-0.46	0.85
	3 & 2	0.6	3.6	0.055	-0.18	0.91
	3 & 3	**0.8**	**8.1**	**0.007**	**0.26**	**0.96**
	3 & 4	0.39	2.1	0.17	-0.48	0.85
2010/2009	1 & 1	-0.19	0.7	0.7	-0.8	0.47
2010/2008	1 & 1	0	1	0.5	-0.77	0.66
	2 & 1	0.24	1.6	0.27	-0.57	0.77

Table A7.26: The ICC2 results for all possible combinations of the BLUPs extracted from the models retained in the confidence sets for the **alert behavioural category** for individuals that were re-sighted in all three years (2008 - 2010; n = 5), 2008 & 2009 (n = 8), 2009 & 2010 (n = 11) and 2008 & 2010 (n = 9) (Table 7.6). The second column shows the combination of models, which begins with the most recent breeding season (e.g. for 2008 - 2010; the model numbers are arranged, 2010, 2009, 2008); the model numbers correspond to those shown in Table 7.6. Significant repeatability estimates are in bold.

Analyses	Model No.	ICC	F	p	upper	lower
2010/2009/2008	1 & 1 & 1	0.38	2.5	0.126	-0.27	0.9
	1 & 1 & 2	0.4	2.6	0.12	-0.26	0.9
	2 & 1 & 1	0.23	1.7	0.24	-0.38	0.86
	3 & 1 & 1	0.35	2.3	0.146	-0.29	0.89
	3 & 1 & 2	0.36	2.4	0.138	-0.28	0.89
2009/2008	1 & 1	0	1	0.5	-0.84	0.7
	1 & 2	0.18	1.4	0.34	-0.71	0.77
2010/2009	1 & 1	0.44	2.4	0.09	-0.24	0.81
	1 & 2	0.4	2.2	0.114	-0.29	0.8
2010/2008	**1 & 1**	**0.78**	**7.2**	**0.006**	**0.26**	**0.95**
	2 & 1	**0.73**	**5.9**	**0.011**	**0.15**	**0.93**

Table A7.27 The relationships between the two response variables and each of the covariates for the individuals that were re-sighted in all three years (n = 5). The analyses were conducted using a Spearman's rank correlation coefficient; significant results are in bold. RV = response variable; CV = covariate. A grey cell indicates that there is no data available for the covariate. The definition of each of the covariates is shown in the legend for Tables A7.10 - A7.18.

		2008		2009		2010	
RV	CV	*p*	r	*p*	r	*p*	r
Alert	ACT	**<0.001**	**0.218**	**<0.001**	**0.292**	**0.008**	**0.136**
	DEN	**0.024**	**0.125**	0.488	0.036	**0.004**	**0.147**
	POOL	0.653	-0.025	0.619	0.026	0.376	0.046
	RAIN	0.59	0.03	0.38	-0.045		
	TEMP	**0.013**	**-0.138**	**0.03**	**-0.112**	0.123	-0.079
	AGE	**0.037**	**0.116**	0.601	0.027	**<0.001**	**-0.171**
	NFN	**0.004**	**-0.159**	0.237	-0.061	**0.029**	**-0.112**
Pup Check	ACT	0.975	-0.002	**0.004**	**0.148**	**<0.001**	**0.31**
	DEN	**0.013**	**0.138**	0.252	-0.059	**0.017**	**0.123**
	POOL	0.322	0.055	0.901	-0.006	0.681	-0.021
	RAIN	0.115	-0.088	0.885	-0.007		
	TEMP	0.735	-0.019	0.92	0.005	0.221	0.063
	AGE	0.341	-0.053	0.817	-0.012	0.11	-0.082
	NFN	**0.002**	**-0.173**	0.581	0.029	0.061	-0.097

Table A7.28: The relationships between the two response variables and each of the covariates for the individuals that were re-sighted in the 2008 & 2009 (n = 8) breeding seasons. The analyses were conducted using a Spearman's rank correlation coefficient; significant results are in bold. RV = response variable; CV = covariate. The definition of each of the covariates is shown in the legend for Tables A7.10 - A7.18.

		2008		2009	
RV	CV	*p*	r	*p*	r
Alert	ACT	**<0.001**	**0.278**	**<0.001**	**0.238**
	DEN	0.144	0.065	0.346	0.042
	POOL	0.777	0.013	0.535	0.028
	RAIN	0.808	-0.011	**0.049**	**-0.088**
	TEMP	**<0.001**	**-0.169**	**0.012**	**-0.112**
	AGE	**0.004**	**0.128**	0.86	0.008
	NFN	**0.02**	**-0.104**	0.133	-0.067
Pup Check	ACT	0.284	0.048	**0.01**	**0.115**
	DEN	**0.013**	**0.111**	0.567	-0.026
	POOL	0.574	0.025	0.564	-0.026
	RAIN	0.166	-0.062	0.156	-0.063
	TEMP	0.533	-0.028	0.104	-0.073
	AGE	0.876	-0.007	0.175	-0.061
	NFN	**0.035**	**-0.094**	0.184	-0.059

Table A7.29: The relationships between the two response variables and each of the covariates for the individuals that were re-sighted in the 2009 & 2010 (n = 11) breeding seasons. The analyses were conducted using a Spearman's rank correlation coefficient; significant results are in bold. RV = response variable; CV = covariate. A grey cell indicates that there is no data available for the covariate. The definition of each of the covariates is shown in the legend for Tables A7.10 - A7.18.

		2009		2010	
RV	CV	*p*	r	*p*	r
Alert	ACT	**<0.001**	**0.216**	**<0.001**	**0.189**
	DEN	0.099	0.063	**0.013**	**0.091**
	POOL	0.641	-0.018	0.863	0.006
	RAIN	0.929	-0.003		
	TEMP	**0.013**	**-0.095**	**0.567**	**-0.021**
	AGE	**0.021**	**0.088**	**0.004**	**-0.104**
	NFN	0.152	-0.055	**0.028**	**-0.08**
Pup Check	ACT	**<0.001**	**0.15**	**<0.001**	**0.304**
	DEN	0.522	-0.024	**0.038**	**0.075**
	POOL	0.68	-0.016	0.332	-0.035
	RAIN	0.337	-0.037		
	TEMP	0.909	-0.004	0.855	-0.007
	AGE	0.205	-0.048	0.556	0.021
	NFN	0.38	0.033	0.132	-0.055

Table A7.30: The relationships between the two response variables and each of the covariates for the individuals that were re-sighted in the 2008 & 2010 (n = 9) breeding seasons. The analyses were conducted using a Spearman's rank correlation coefficient; significant results are in bold. RV = response variable; CV = covariate. A grey cell indicates that there is no data available for the covariate. The definition of each of the covariates is shown the legend for Tables A7.10 - A7.18.

		2008		2010	
RV	CV	*p*	r	*p*	r
Alert	ACT	**<0.001**	**0.262**	**<0.001**	**0.122**
	DEN	0.855	0.008	0.563	0.021
	POOL	0.345	0.04	0.711	-0.013
	RAIN	0.5	0.029		
	TEMP	0.163	-0.059	0.277	-0.039
	AGE	**<0.001**	**0.141**	**<0.001**	**-0.165**
	NFN	0.244	-0.05	0.794	0.009
Pup Check	ACT	0.295	0.045	**<0.001**	**0.267**
	DEN	0.423	0.034	**0.017**	**0.086**
	POOL	0.535	0.026	0.434	0.028
	RAIN	**0.038**	**-0.088**		
	TEMP	0.242	0.05	0.809	0.009
	AGE	**0.024**	**-0.096**	0.941	0.003
	NFN	0.26	-0.048	0.122	-0.056

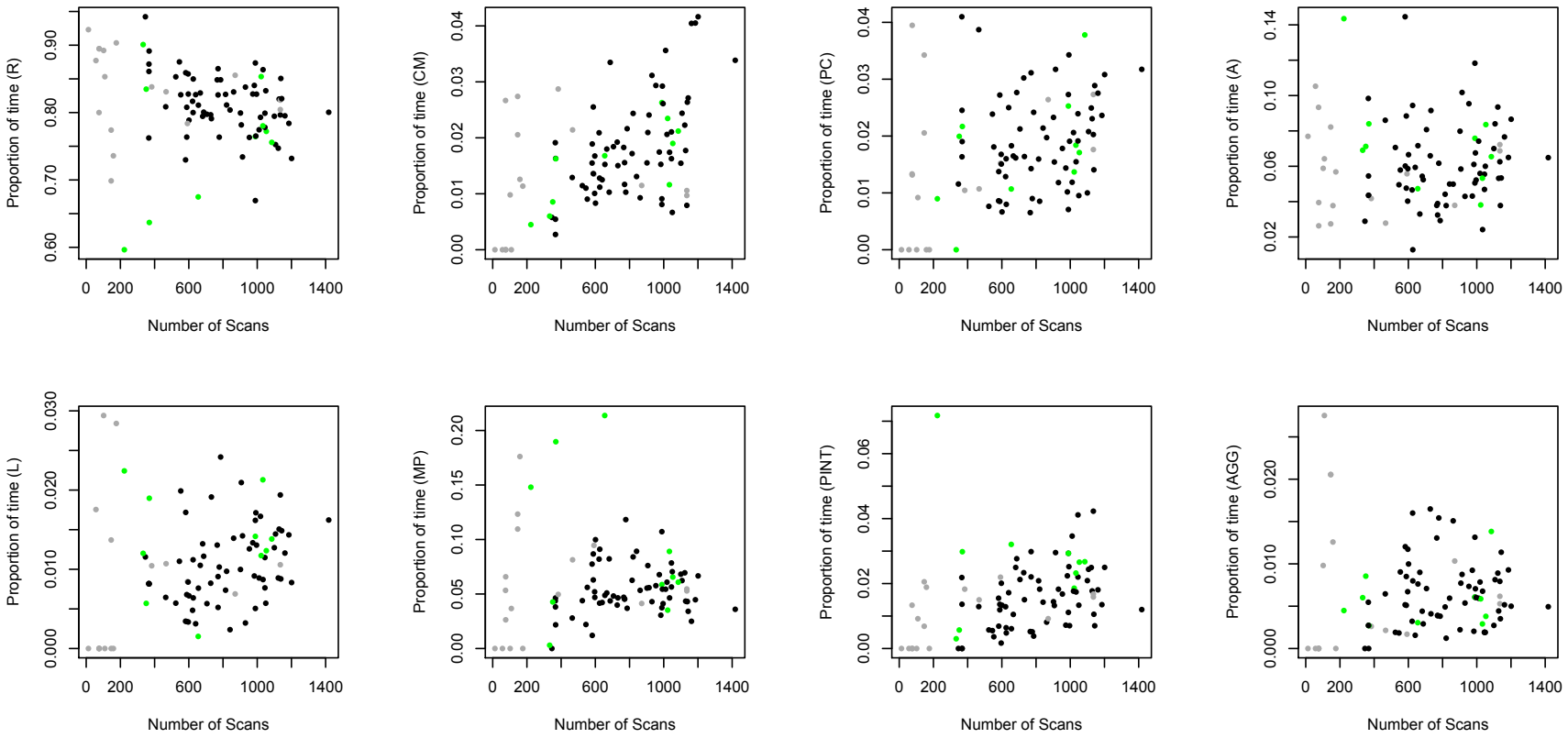


Figure A7.1: The gross activity plots for the resting (R), comfort movement (CM), pup check (PC), alert (A), locomotion (L), presenting & nursing (MP), pup interactions (PINT) and aggression (AGG) behavioural categories for all individuals (n = 91) for all 3 years combined (2008 - 2010). The individuals with ≤ 200 scan samples are shown in dark grey (n = 11), the 10 additional individuals that were omitted from the dataset are shown in green (see Section 7.3.2 for more information). The black data points show the individuals (n = 70) that were retained in the gross dataset.

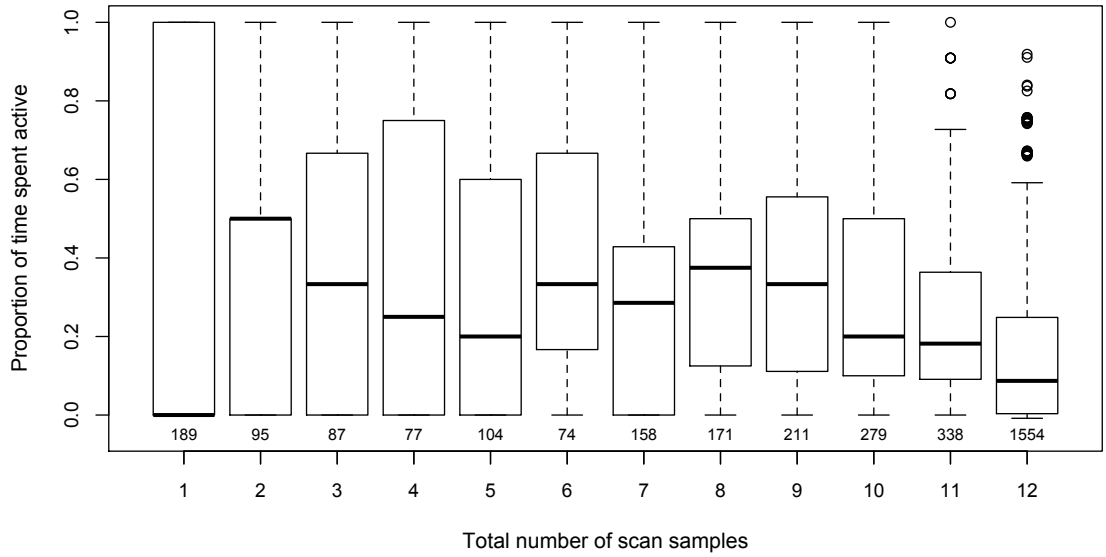
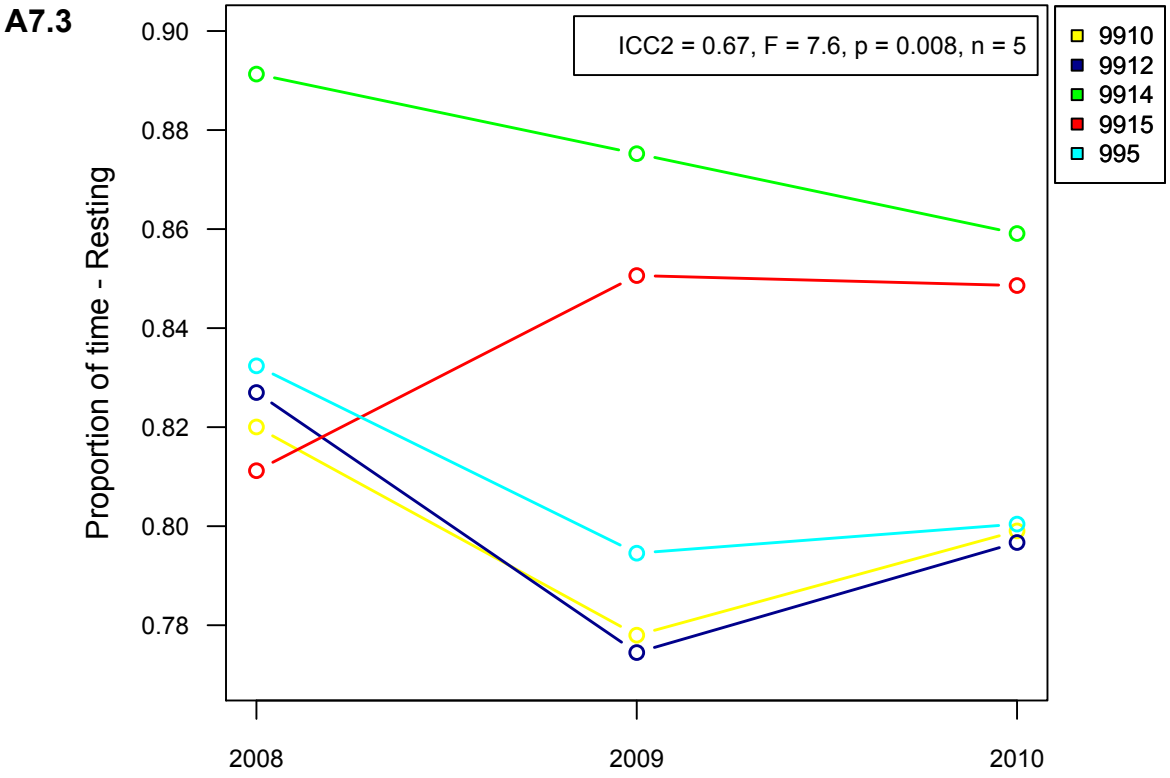


Figure A7.2: The pup activity plotted against the total sample size of scans per hour for the pups of females re-sighted in two or more breeding seasons (N = 18). The number of times that the 'total number of scans' were recorded, is noted on the inside of the x-axis.

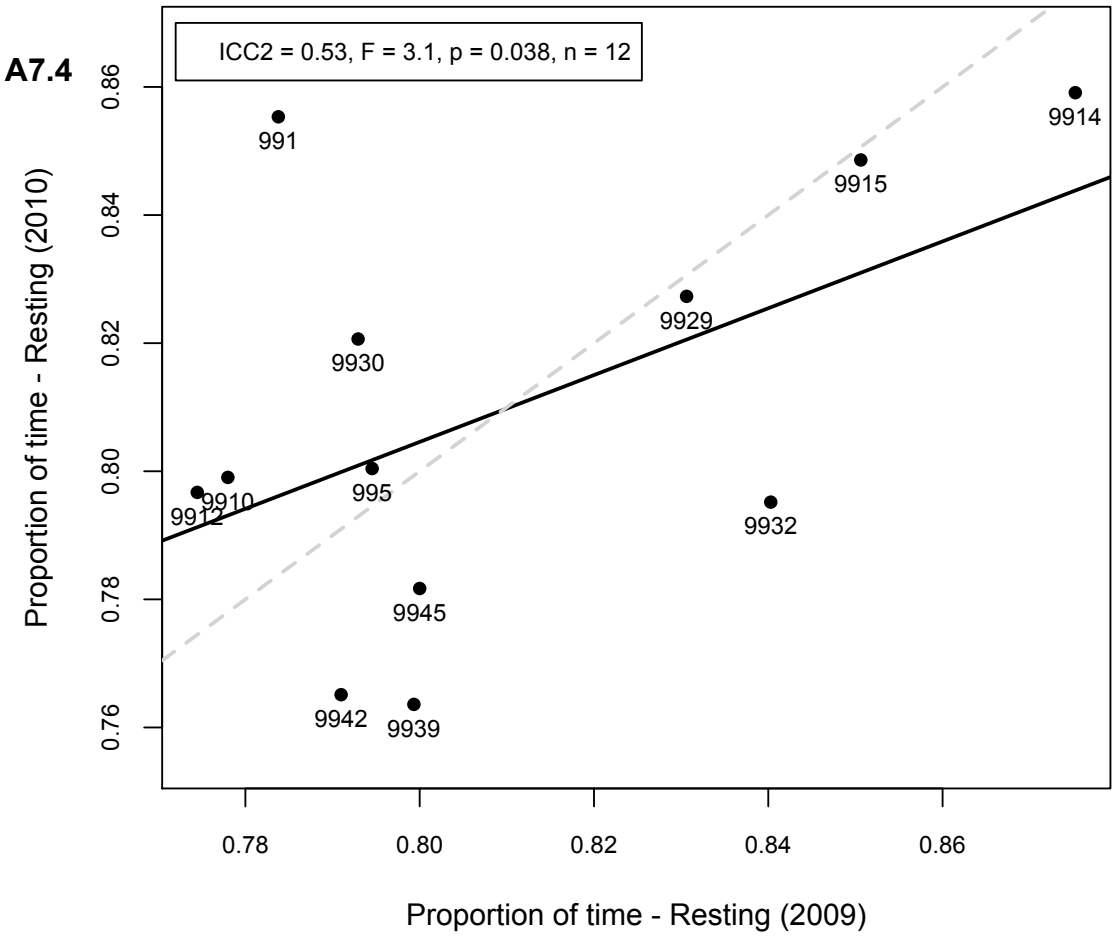
The following 3 pages show:

Figures A7.3 - A7.8: The plots of the significant repeatability estimates for: **A7.3, A7.4**). Resting (2008 - 2010, 2008 & 2009, respectively), **A7.5**). Comfort movement (2008 & 2009), **A7.6, A7.7, A7.8)**. Pup interactions (2008 - 2010, 2008 & 2009, 2009 & 2010, respectively). ICC2 results are shown in the legend within each of the plots. For the figures presenting three years of data the individual ID numbers are shown in the legend out-with the plot and are colour coded to the plotted lines. For the figures presenting two years of data the individual ID numbers are given for each data point. The line of best fit (black solid line) and the 1:1 line (grey dashed line) are presented in the pairwise plots.

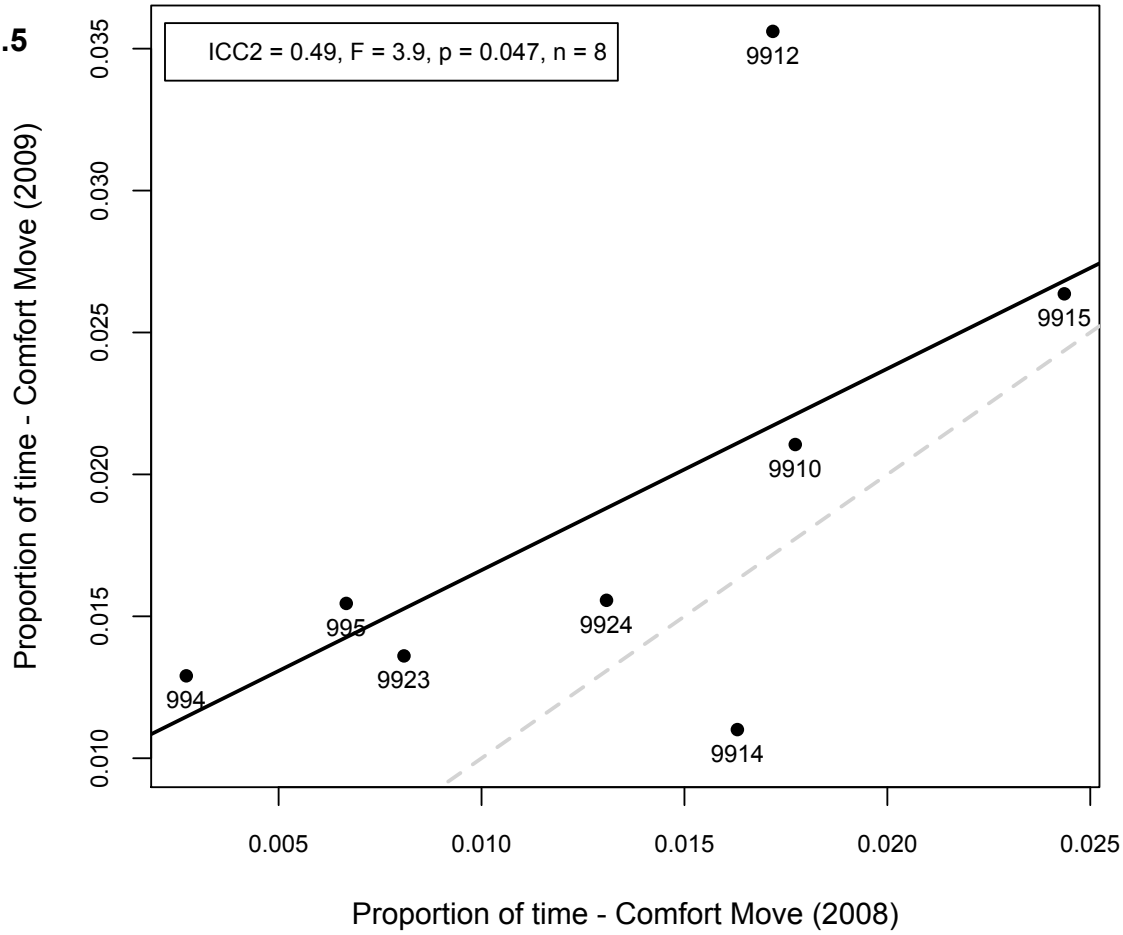
A7.3


ICC2 = 0.67, F = 7.6, p = 0.008, n = 5
9910
9912
9914
9915
995
Proportion of time - Resting
0.90
0.88
0.86
0.84
0.82
0.80
0.78
2008
2009
2010

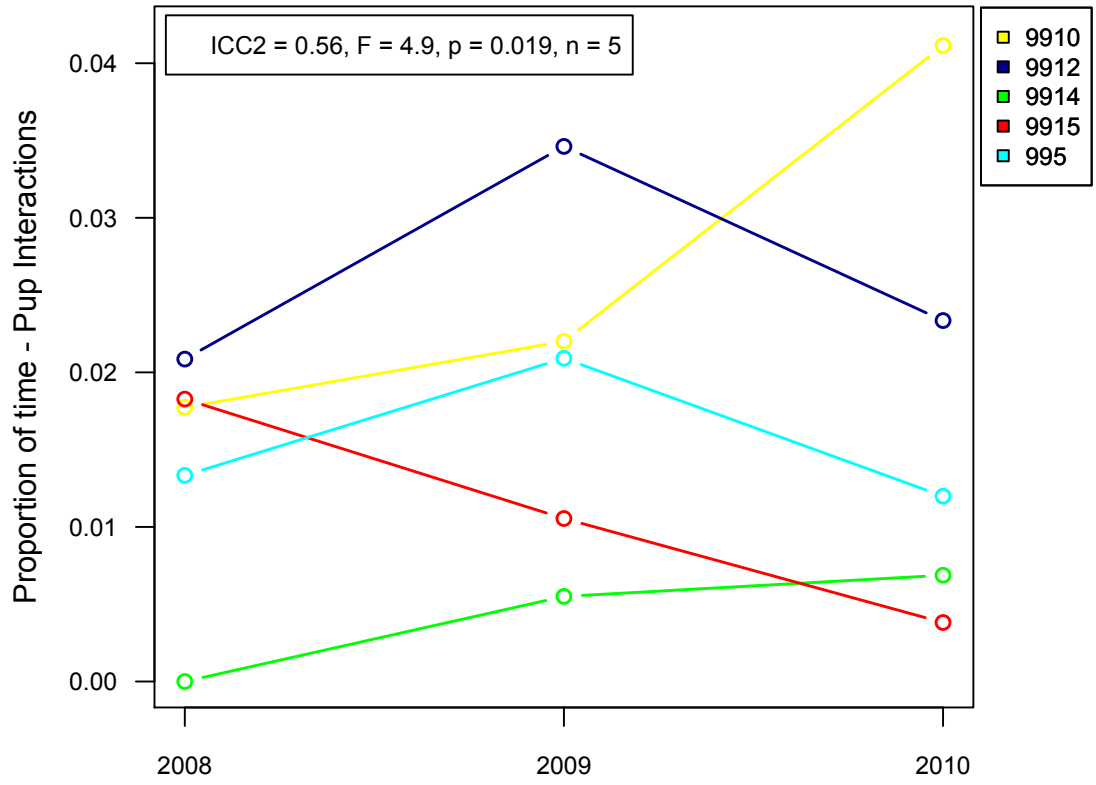
A7.4


ICC2 = 0.53, F = 3.1, p = 0.038, n = 12
991
9914
9915
9929
9930
995
9910
9912
9932
9945
9942
9939
Proportion of time - Resting (2010)
0.86
0.84
0.82
0.80
0.78
0.76
0.78
0.80
0.82
0.84
0.86
Proportion of time - Resting (2009)

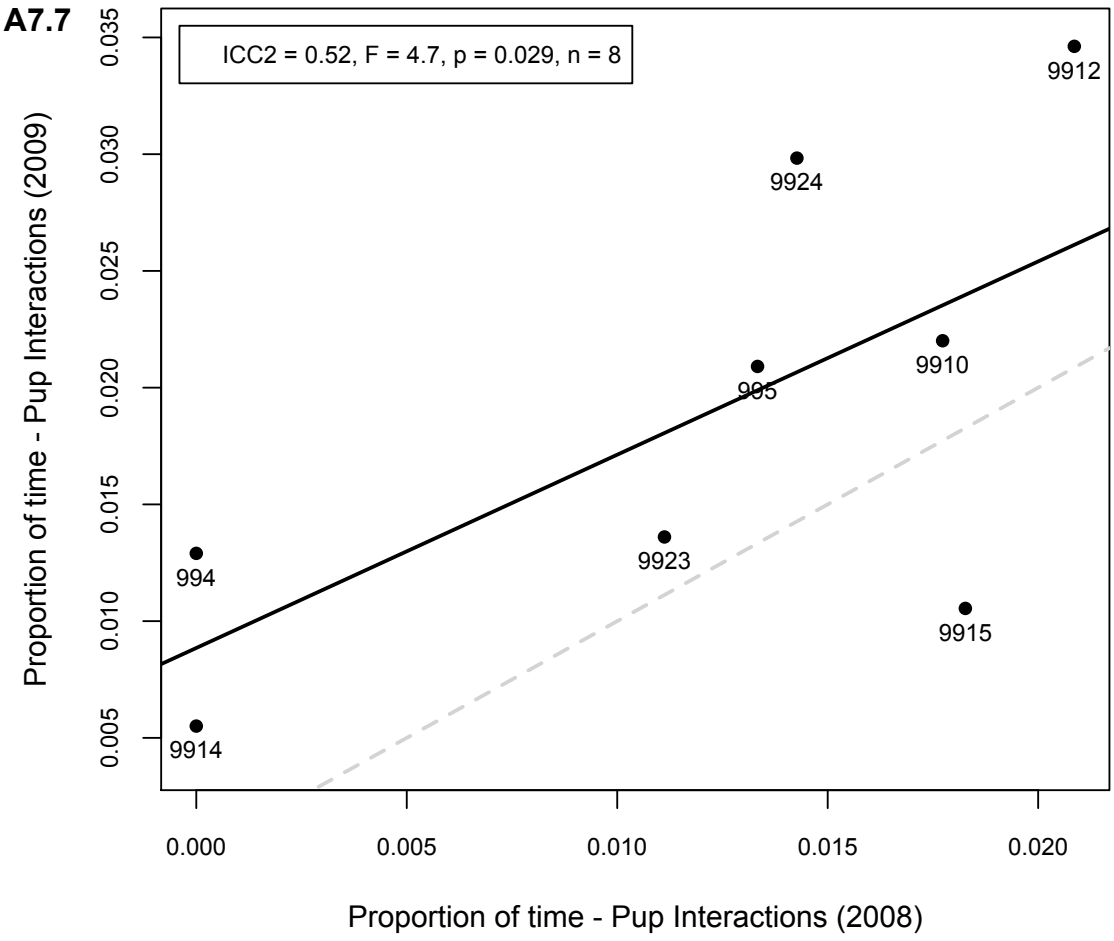
A7.5


ICC2 = 0.49, F = 3.9, p = 0.047, n = 8
9912
9915
9910
9924
995
9923
994
9914
0.035
0.030
0.025
0.020
0.015
0.010
0.005
0.010
0.015
0.020
0.025
Proportion of time - Comfort Move (2009)
Proportion of time - Comfort Move (2008)

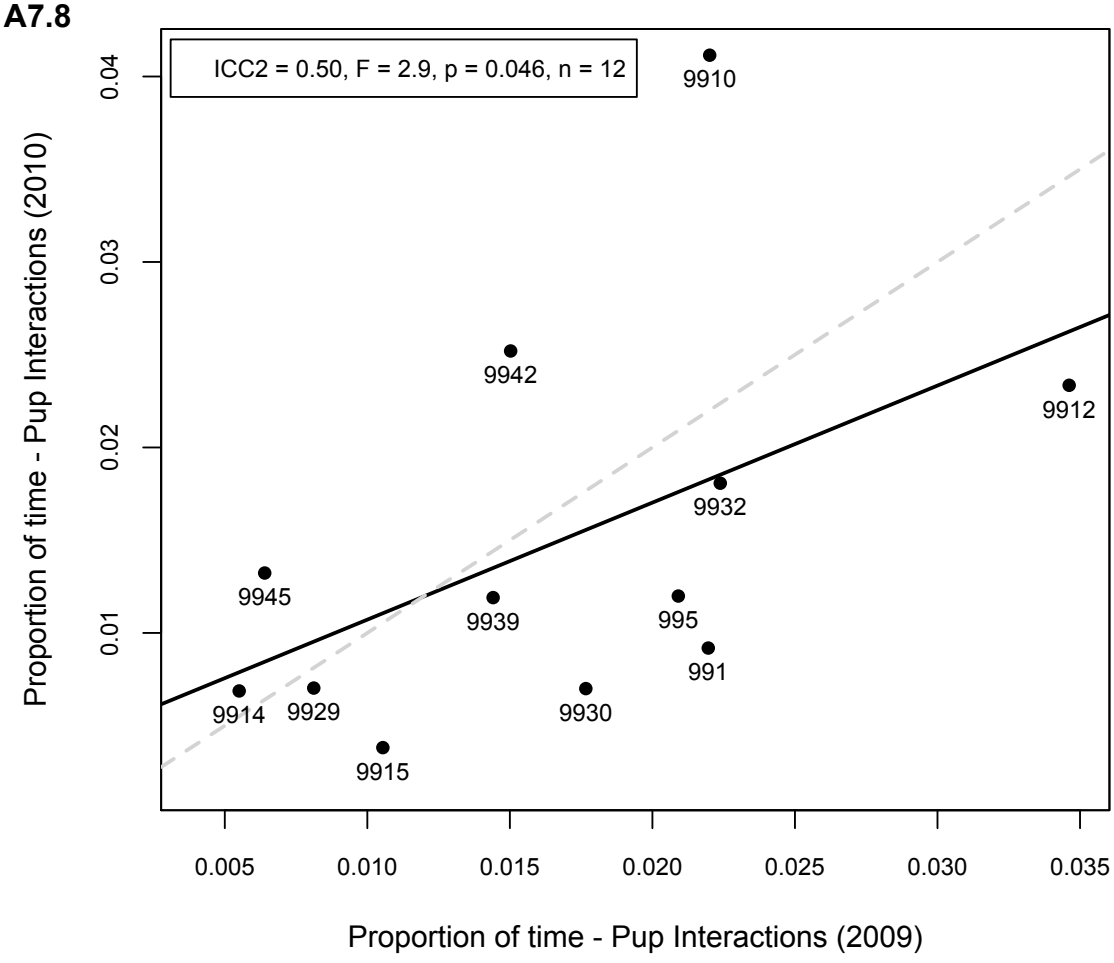
A7.6


ICC2 = 0.56, F = 4.9, p = 0.019, n = 5
9910
9912
9914
9915
995
0.04
0.03
0.02
0.01
0.00
2008
2009
2010
Proportion of time - Pup Interactions

A7.7


ICC2 = 0.52, F = 4.7, p = 0.029, n = 8
Proportion of time - Pup Interactions (2009)
Proportion of time - Pup Interactions (2008)
0.005
0.010
0.015
0.020
0.025
0.030
0.035
0.000
0.005
0.010
0.015
0.020
9912
9924
9910
995
9923
994
9915
9914

A7.8


ICC2 = 0.50, F = 2.9, p = 0.046, n = 12
Proportion of time - Pup Interactions (2010)
Proportion of time - Pup Interactions (2009)
0.01
0.02
0.03
0.04
0.005
0.010
0.015
0.020
0.025
0.030
0.035
9910
9942
9912
9932
9945
9939
995
991
9914
9929
9930
9915

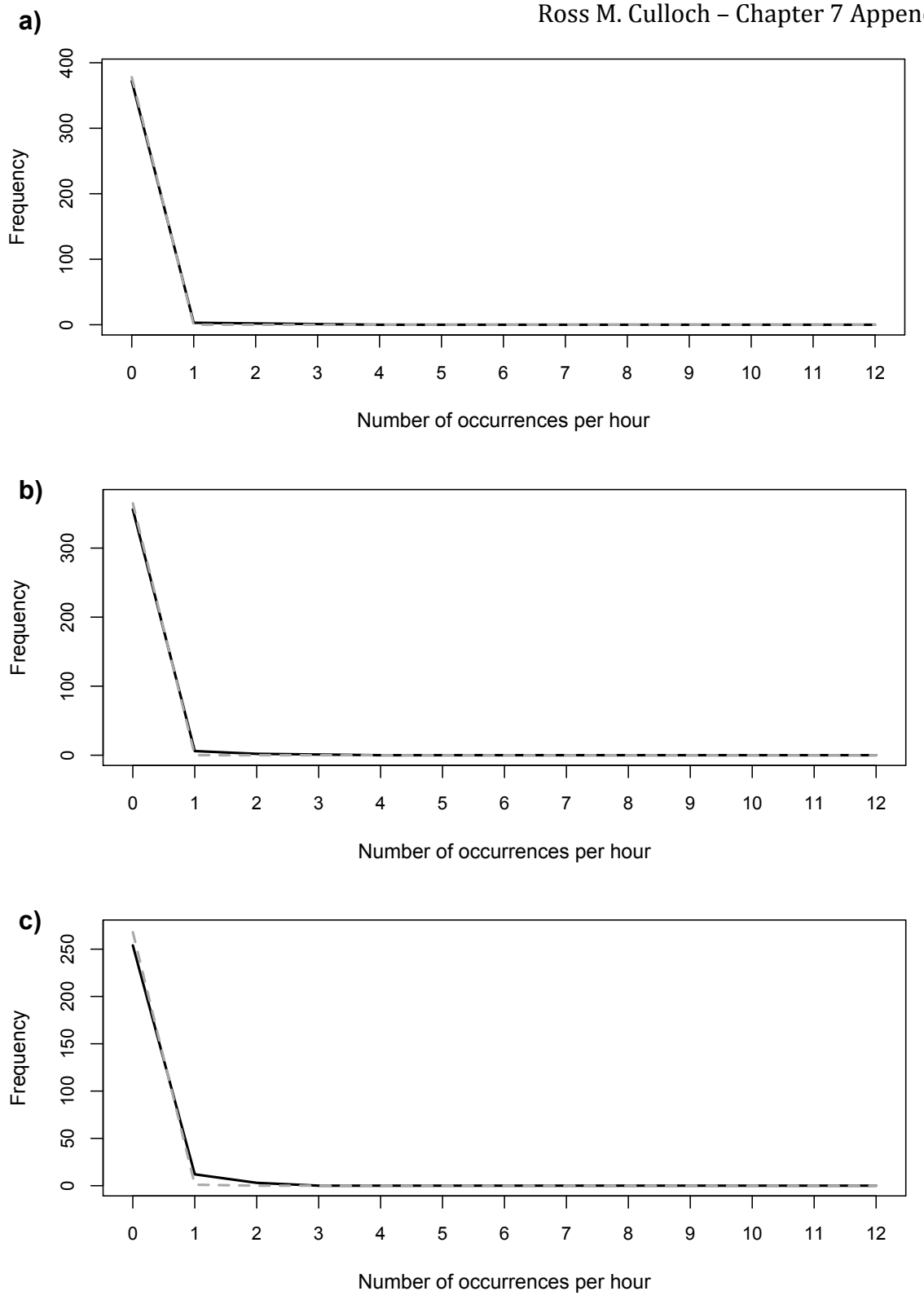


Figure A7.9: The predicted (dashed grey line) and the observed (solid black line) values for the pup check behavioural category for the **a)** 2008 **b)** 2009 (2008 & 2009 re-sighted individuals) and **c)** 2010 (2008 - 2010 re-sighted individuals) breeding seasons. See Chapter 5, Section 5.3.8 for more details on how these plots were constructed.

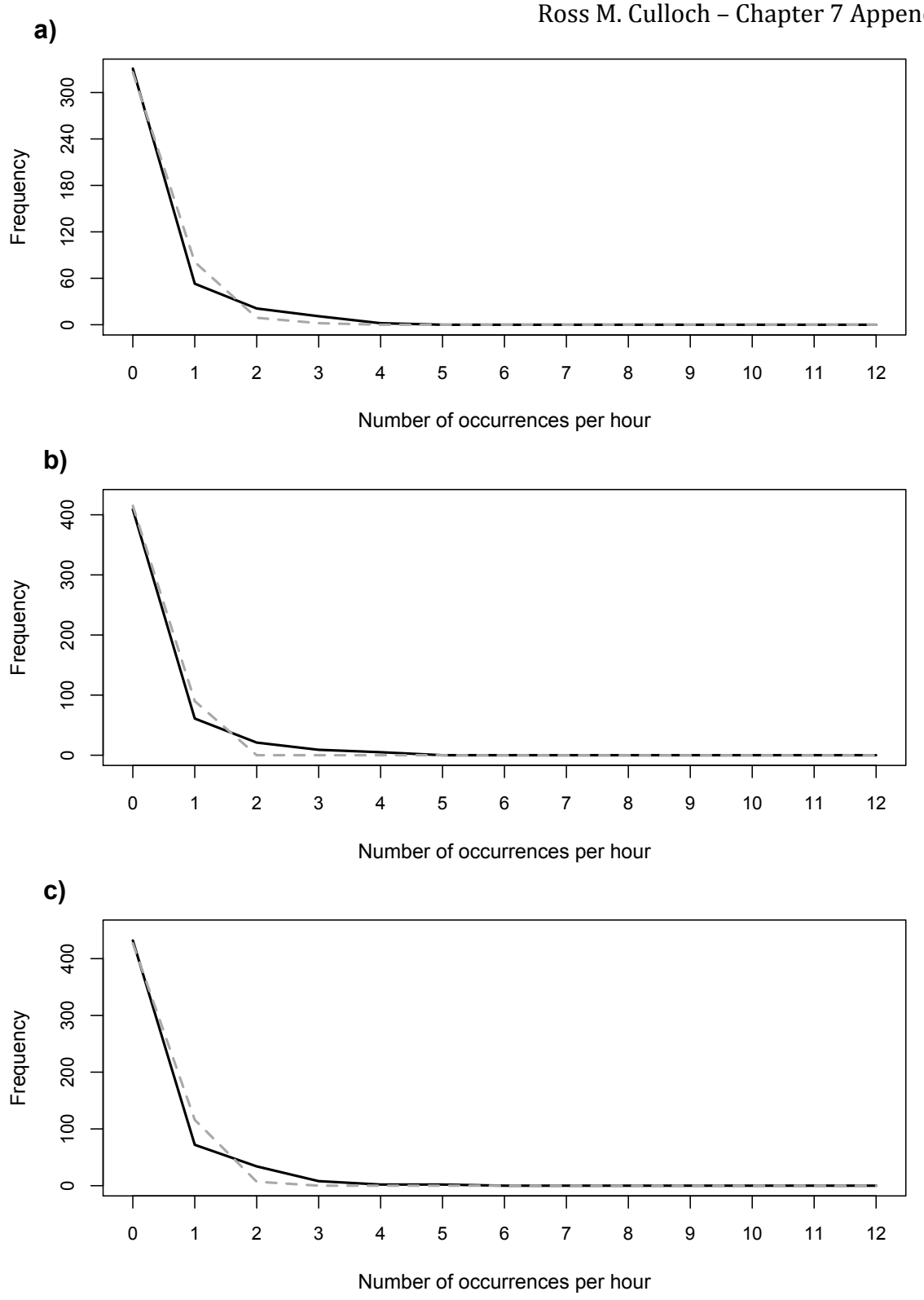


Figure A7.10: The predicted (dashed grey line) and the observed (solid black line) values for the alert behavioural category for the **a)** 2008 (2008 & 2010 re-sighted individuals) **b)** 2009 (2009 & 2010 re-sighted individuals) and **c)** 2010 (2008 & 2010 re-sighted individuals) breeding seasons. See Chapter 5, Section 5.3.8 for more details on how these plots were constructed.

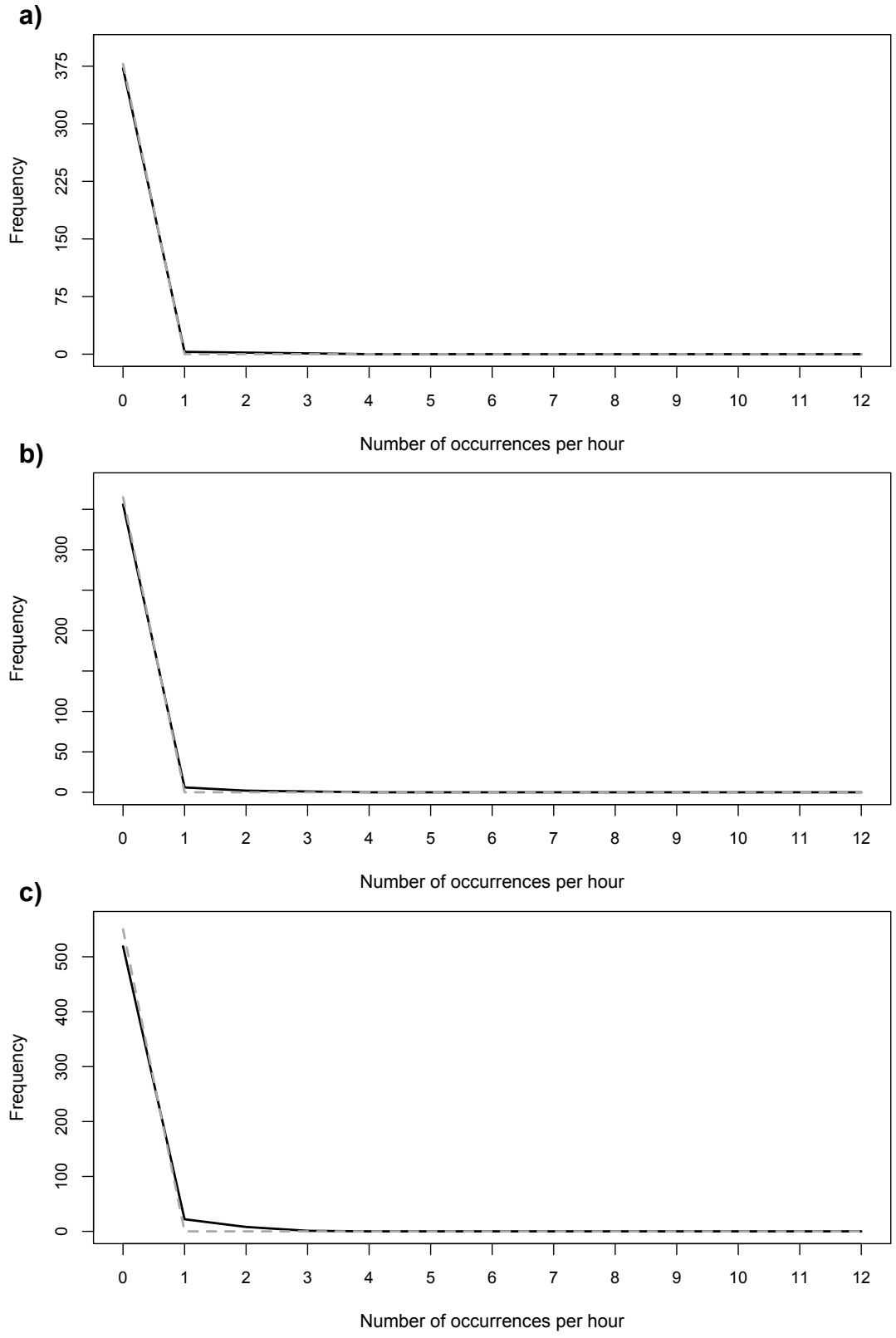


Figure A7.11: The predicted (dashed grey line) and the observed (solid black line) values for the pup check behavioural category for the **a)** 2008 **b)** 2009 (2008 & 2009 re-sighted individuals) and **c)** 2010 (2008 - 2010 re-sighted individuals) breeding seasons. See Chapter 5, Section 5.3.8 for more details on how these plots were constructed.

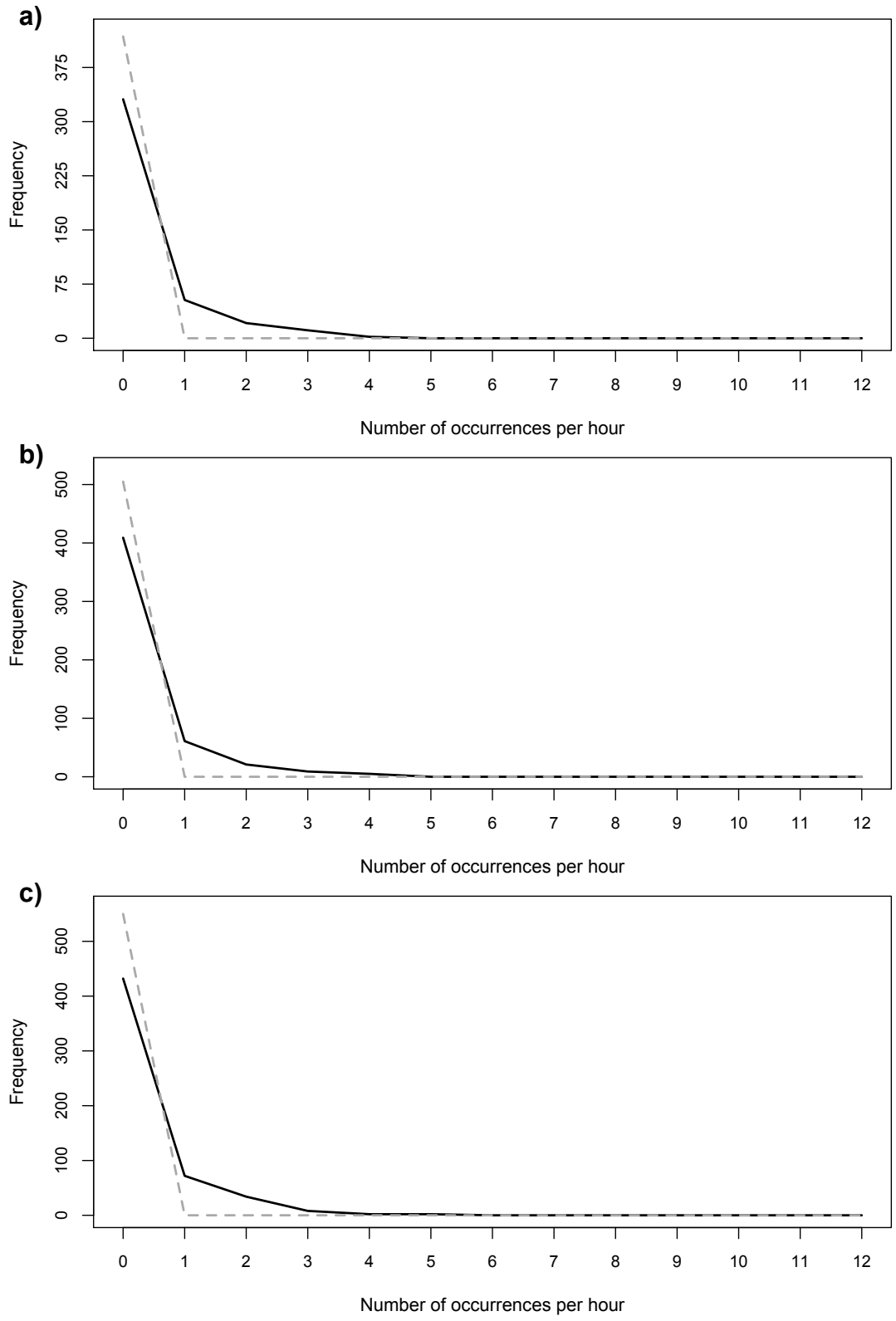


Figure A7.12: the predicted (dashed grey line) and the observed (solid black line) values for the alert behavioural category for the **a)** 2008 (2008 & 2010 re-sighted individuals) **b)** 2009 (2009 & 2010 re-sighted individuals) and **c)** 2010 (2008 & 2010 re-sighted individuals) breeding seasons. See Chapter 5, Section 5.3.8 for more details on how these plots were constructed.

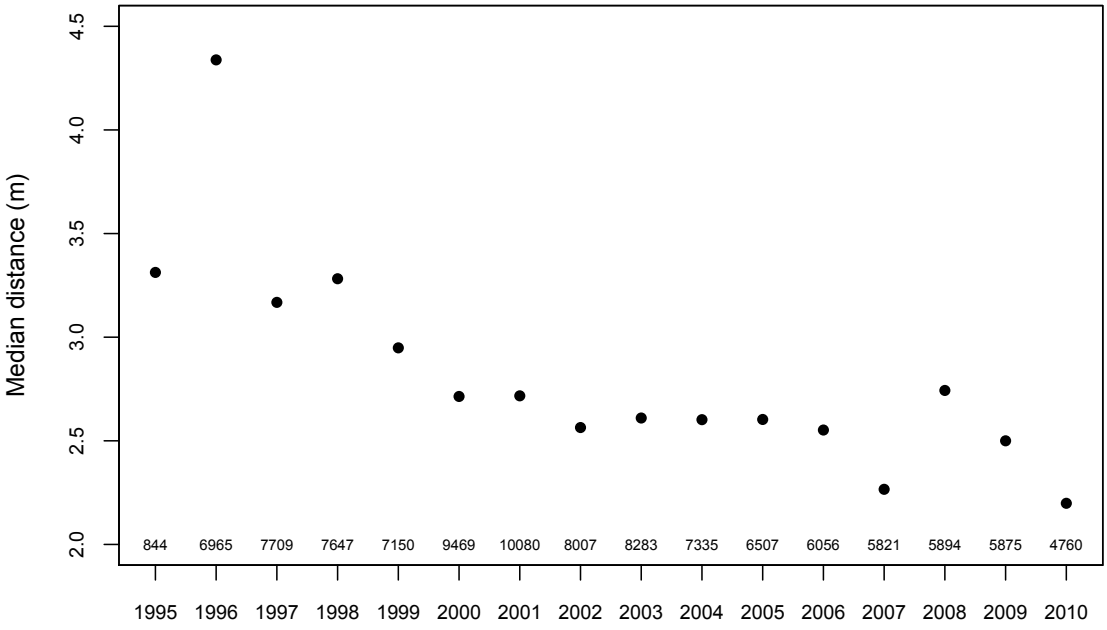


Figure A7.13: The median distance between females and the nearest pool of water in the SA for the 1995 to 2010 breeding seasons. The year is shown on the x-axis, the pool coverage used in all years was from the 1994 breeding season. Each data point represents all females within the SA, for all maps available for the given breeding season; pseudoreplication is not accounted for. The total number of data points (females' locations) that comprise the median are shown on the inside of the x-axis.

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An in-field experimental test of pinniped behavioral types

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ABSTRACT

There has been extensive recent interest in the concepts of behavioral types, behavioral syndromes, and personalities in nonhuman animal species. Evidence for behavioral types now exists from a wide range of taxa, from mollusks to mammals. However, marine mammals are poorly represented in this literature. Here, we describe an in-field experimental test of behavioral types in breeding gray seals, using a remotely controlled vehicle to deliver a standardized test stimulus to target individuals. We report on the design and implementation of this test and on the behavioral responses of individuals. Analysis of behavioral responses from both males and females revealed consistent individual differences across tests, suggesting that this is a practical and viable technique for determining individual variation in behavioral type in the field. Despite extensive literature on behavioral types, studies of behavioral types in wild populations remain rare. It is, therefore, important to develop ways to identify and quantify the existence of behavioral types in natural populations, because only by doing this, can we hope to ascertain the ecological and evolutionary relevance of behavioral types.

Key words: consistent individual differences, personality, behavioral syndromes, in-field experimental test, breeding behavior, gray seal, *Halichoerus grypus*.

Within the behavioral and evolutionary ecology literature there has been extensive recent interest in the concepts of behavioral types, behavioral syndromes, and personalities in nonhuman animal species (Gosling 2001; Sih *et al*. 2004*a*, *b*; Dingemanse and Réale 2005; Bell 2007*a*, *b*; Réale *et al*. 2000, 2007; Martin and Réale 2008; Sih and Bell 2008). These concepts generally describe patterns of consistency in individual differences in behavior over time, unrelated to age and sex class differences (Martin and Réale 2008, Sih and Bell 2008, Bell *et al*. 2009, Biro and Stamps 2010). Studies of behavioral types measure the behavior of individuals on more than one occasion and apply measures of repeatability to quantify the proportion of

within-individual variance relative to among-individual variance (Boake 1989, Bell *et al*. 2009).

There is now evidence of behavioral types in a remarkable range of taxa, from mollusks to mammals (Réale *et al*. 2007, Smith and Blumstein 2008, Bell *et al*. 2009). However, there are few such studies on marine mammals. Highfill and Kuczaj II (2007) examined temporal consistency in human observer judgements of captive bottlenose dolphin (*Tursiops truncatus*) personality characteristics. In the wild, there are studies demonstrating individual foraging specializations (Gazda *et al*. 2005, Duffy-Echevarria *et al*. 2008, Mann *et al*. 2008), individual differences in early social development (Gibson and Mann 2008) and individually specific vocalizations (*e.g*., Janik *et al*. 2006) in bottlenose dolphins. There appear to be even fewer studies indicating behavioral types among pinnipeds. Sanvito and Galimberti (2003) demonstrated individually repeatable male vocalizations in *Mirounga* spp., and Lang *et al*. (2009) provided evidence of individually repeatable reproductive performance in gray seals (*Halichoerus grypus*). However, to our knowledge only Twiss and Franklin (2010) have explicitly set out to test for evidence of behavioral types in marine mammals in the field. Why are marine mammals underrepresented in the literature on behavioral types, especially as most who work closely with marine mammals would probably agree with the statement that their study animals are very "individual"? In terms of field based studies this is most likely explained by the aquatic environment in which marine mammals spend all or most of their time, as well as the difficulties associated with repeatedly observing or testing specific individuals *in situ*. Field studies of behavioral types are undoubtedly more challenging and often fraught with more difficulties compared to laboratory or captive based studies, and captive studies of marine mammals are limited by logistics, costs, and ethical considerations. However, it is essential to develop *in situ* techniques for identifying behavioral types of animals in their natural environment in order to begin to appreciate the broader ecological and evolutionary relevance of animal personalities (Sih *et al*. 2004*a*, *b*; Dingemanse and Réale 2005; Bell 2007*a*, *b*; Réale *et al*. 2007; Sih and Bell 2008; Bell *et al*. 2009; Biro and Stamps 2010). When repeated observations of known individuals can be made, it is possible to gather evidence for behavioral types purely by behavioral observations in the wild (Twiss and Franklin 2010). However, purely observational studies are open to criticism, such as the fact that study animals will be exposed to a complex range of differing stimuli. Therefore, there is a need for a more experimental, controlled, and standardized testing of behavioral type that can be applied in the field. However, this raises challenges in terms of the delivery of a standardized stimulus to target individuals *in situ* while avoiding excessive disturbance in the process of placing the stimulus. As part of our long-term study of individual variation in breeding gray seals (Pomeroy *et al*. 1994, 1999, 2001; Twiss *et al*. 1994, 2006*a,* 2006*b*) we aimed to develop a standardized protocol for eliciting quantifiable behavioral responses from individual seals over repeated trials. Here, we describe our in-field test of behavioral type for breeding gray seals that achieves a standardized stimulus, delivered to the target seal without causing excessive disturbance.

Methods

Study Colony and Background to Gray Seal Breeding Behavior

The experimental tests were conducted on the gray seal breeding colony of North Rona (59°06'N, 05°50'W), Scotland. The North Rona study site is described in

detail elsewhere (Twiss *et al*. 1994, 2006*a*; Pomeroy *et al*. 1999), but the main point of relevance here is that the colony consists of undulating grassy terrain with slopes ranging from 0° to approximately 40°. These grassy slopes are punctuated by irregularly spaced boulders, rocky outcrops, remnants of old stone walls, and small pools of water of varying surface area ($\bar{x} = 0.77$ m^2, SD = 2.51 m^2, range = 0.011–70.46 m^2, $n = 1{,}057$ pools).

Gray seals gather at North Rona during the autumn to breed (Pomeroy *et al*. 1994, 2001, Twiss *et al*. 1994, 2000, 2006*a*, *b*). Although nursing females tend to aggregate around pools of water on the colony (Pomeroy *et al*. 1994, 2001; Twiss *et al*. 2000), they maintain a distance of at least two adult body lengths from their nearest neighbors (median nearest neighbor distances = 4.36 m; Pomeroy *et al*. 1994, Twiss *et al*. 2000). Females generally remain close to their pups throughout lactation, but may occasionally commute between their pup and pools of water (Redman *et al*. 2001, Twiss *et al*. 2006*a*). Males are more widely dispersed amongst the female groups, with median nearest male neighbor distances of 15.6 m (Twiss *et al*. 1994). The distribution and activity of males is primarily determined by female distribution, as males compete to maintain loose home ranges amongst the groups of females (Twiss *et al*. 1994, 1998, 2006*a*). Both males and females can be individually identified by pelage and scarring patterns (Pomeroy *et al*. 1994, Twiss *et al*. 1994, Redman *et al*. 2001).

Remote Control Vehicle: Experimental Protocol

Our aim was to devise a means of repeatedly delivering a standardized stimulus to target seals in their natural habitat to allow quantitative analysis of between individual variation and within-individual consistency in behavioral responses. We also wished to place the stimulus by the target seal with minimal disturbance. To achieve this we used a modified remote controlled vehicle (RCV) to approach seals and to remotely trigger a stimulus (Fig. 1). Details of the design and construction of the RCV are provided in the Supporting Information.

All tests were performed between 0700 and 1100 GMT on relatively dry (no rain or light drizzle) days with wind speeds less than Beaufort scale force 6 (*ca.* 24 kn).

Females—During the 2009 breeding season on North Rona the RCV was used to test 26 females. From the total, 20 females were tested twice, once early in lactation, and once late in lactation. The aim was to achieve a standard timing with respect to birthing, with repeated tests on individuals ideally being performed 10 d apart, at 4 and 14 d postpartum. The sound stimulus used was a "wolf" call (duration 4.15 s). This was selected as it represented a potentially mildly alarming but natural auditory stimulus, that gray seals on North Rona would not have been exposed to previously, and was, therefore, also a novel stimulus. Initial trials of a range of natural animal calls were made during the 2008 breeding season to discover which sound elicited a reasonable range of alert responses from seals, but were not so alarming as to cause seals to move away. The wolf call registered 75 dB at 1 m distance from the speaker, and approximately 65 dB at 3 m, the typical distance between the speaker and the target seal. The protocol used for testing females with the RCV was:

1. The operator of the RCV was positioned at least 50 m downwind from the intended target seal, to prevent the seal from reacting to the operator. The operator, however, had a reasonable vantage point with which to view both the target seal and the approach to the target seal.

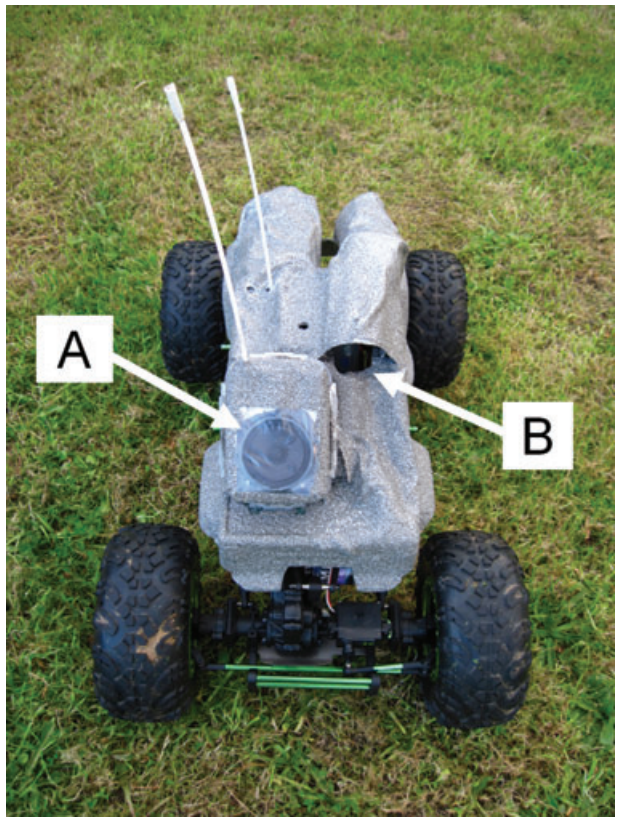

Figure 1. Photograph of the RCV with fiberglass cover in the field. (A) Box containing sound stimulus electronics with own antenna. (B) On-board video camera. The approximate dimensions of the RCV were: height = 225 mm, length = 645 mm, width: 375 mm, wheelbase = 460 mm, weight 5,300 g.

2. The RCV was driven to within 1–2 body lengths (*ca.* 3 m) of the target seal. The RCV was driven in a circuitous route, with final approach to the target seal made at right angles to an imaginary straight line between the target seal and operator. Thus, the RCV approached the target seal from the side as viewed from the operator's perspective. Again, this ensured that it was possible to discern whether target seals were looking at the RCV or the observer. Approaches were ideally standardized with respect to mother-pup orientation, with the pup being behind the mother. This typically occurred, because mothers usually placed themselves between their pup and any perceived threat.
3. The RCV was brought to a halt and remained stationary and silent for 5 min. This was for the seals to acclimate to the presence of the RCV.
4. The first sound stimulus was triggered, followed by a 2 min pause.
5. The second sound stimulus was triggered, followed by a 2 min pause.
6. The final sound stimulus was triggered, followed by a 2 min pause.

7. The vehicle was reversed away from the target seal, and returned to the operator.
8. The RCV was, therefore, stationary within close proximity to each target seal for a total of 11 min per test. One entire test, including approach and retreat took approximately 15 min to complete. The call was repeated three times in each test to ensure that representative responses were obtained (responses to a single iteration could potentially have been influenced by stochastic environmental stimuli) and to provide the potential to look for evidence of habituation or sensitization. The entire process was recorded using an Oregon Scientific ATC3000 action video camera installed on the RCV (see Supporting Information) to provide close-up footage of seal responses, and a second digital video camera stationed with the operator to record not only the target seal's responses, but also those of neighboring seals to provide context. The second camera used was a Canon DC40 (with 10× optical zoom), which recorded onto 8 cm DVD-R (1.4 Gb, 30 min) and was mounted on a Manfrotto tripod.

Females targeted on a specific day were selected such that no other neighboring females were exposed to the test on the same day in order to minimize the chance of prior exposure and habituation or sensitization. All females tested were geographically separated by at least 20 m.

Video footage of the tests was later analyzed to extract key behavioral metrics. The main behavioral metric used was the number of pup checks performed by the target seal during the 11 min of the test. Pup checks are where the mother is alert, with her head off the ground and making a definite and directed look at her pup (Kovacs 1987). A single pup check was defined as commencing when the mother was alert and oriented her head clearly towards the pup, and ending when the mother oriented her head away from the pup. A pup-check is typically a clear and discrete behavior which is readily observed when both mother and pup are in clear view. In addition we recorded other behavioral responses, including; locomotion towards or away from the RCV, sniffing or other inspection of the RCV, open mouth threats towards the RCV, and aggressive contact with the RCV (lunges and bites making actual contact with the RCV). The on-board video camera and the camera stationed with the observer provided clear footage of target seals' responses (see supplementary video footage). For comparison with behavioral responses to the RCV test, we determined baseline pup checking rates from half-hour video focal samples of 11 mothers (of which four were individuals exposed to the RCV test) recorded on days when no RCV tests were being performed.

Males—Initial trials using the same protocol as described for females above proved unsuccessful with males. Males very rarely remained close to the RCV for the entire 11 min of the test. Therefore, a different protocol was established for males. This involved simply approaching the target male with the RCV in a similar fashion to that described above with respect to positioning of the observer and direction of approach. The behavioral metric used for males was a ranking based on the overall response of the male upon approach of the RCV. Male response was ranked on a scale of −5 to +5 (Table 1, see also supplementary video footage). Using this protocol a total of 17 males were tested, of which 12 were exposed to a second test. Individual tests for males lasted for approximately 3 min, with the RCV being in close proximity to the male for a maximum of 1 min. The remaining duration of the test depended upon the nature of the terrain that was navigated on the approach to, and departure from, the male. Males were tested on a more *ad hoc* basis, with intertest intervals

Table 1. Description of rankings given to male responses to the RCV test. Descriptions pertain to males' initial responses upon becoming aware of the approach of the RCV.

Rank	Description
−5	Male moves away from the RCV at top speed. Locomotion involves rapid directed movement with undulations of the entire body, with the abdomen and thorax lifting clear of the ground
−4	Male moves at moderate-fast speed away from the RCV. Movement involves a mixture of faster (−5) and slower (−3) forms of locomotion.
−3	Male moves at moderate speed away from the RCV. Locomotion involves use of fore-flippers and undulations of thorax/abdomen, but body retains contact with the ground.
−2	Male moves at slow-moderate speed away from the RCV. Movement involves a mixture of faster (−3) and slower (−1) forms of locomotion, with male frequently turning to look at the RCV.
−1	Male cautiously and slowly retreats from the RCV. Locomotion involves use of fore-flippers only.
0	No change in male behavior or location.
1	Male cautiously and slowly approaches the RCV. Locomotion involves use of fore-flippers only.
2	Male moves at slow-moderate speed towards the RCV. Movement involves a mixture of faster (3) and slower (1) forms of locomotion, with male frequently pausing to look at the RCV.
3	Male approaches the RCV at moderate speed. Locomotion involves use of fore-flippers and undulations of thorax/abdomen, but body retains contact with the ground.
4	Male moves at moderate-fast speed towards the RCV. Movement involves a mixture of faster (5) and slower (3) forms of locomotion.
5	Male approaches the RCV at full speed. Locomotion involves rapid directed movement with undulations of the entire body, with the abdomen and thorax lifting clear of the ground.

being between 4 and 10 d. This is because the primary focus for the research was female behavior, and it was initially suspected that males might attack and damage the RCV. Therefore, all male tests were left until the latter part of the breeding season. All males tested were at least 50 m from their nearest male neighbor at the time of testing.

Statistical Approach

We were unable to ensure equivalent intertest durations for all individuals due to weather conditions or other field work commitments; therefore, we performed two analyses to assess whether the time between the first and second tests influenced how repeatable individual responses were across the two tests: (1) To assess the potential effect of time between tests on repeatability we first extracted residuals from a linear regression of the behavioral metrics (pup-check for females, and response to RCV for males; Table 1) from test two on those from test one. These residuals represent the degree of deviation from the line of best fit and, therefore, a measure of the difference in individuals' responses to test one and test two. Then, we performed a second linear regression to examine whether the time between tests showed any significant

relationship with these residuals (degree of difference in individuals' responses to test one and test two). (2) To assess the potential effect of time between tests on deviation from absolute agreement in individual responses over the two tests we first extracted residuals from a fitted 1:1 line (intercept = 0, slope = 1) plotted through the behavioral metrics from tests one and two. These residuals correspond to the degree of deviation from a hypothetical line representing exact agreement between the measures for test one and test two. Then, we performed a second linear regression to examine whether the time between tests showed any significant relationship with these residuals. Approaches (1) and (2) are similar but subtly different, in that the latter (2) is based on a presumption of absolute agreement, *i.e.*, that seals will perform the behavior to the same extent in each test, while the former (1) allows for a change in levels of performance of the behavior across the study group (*i.e.*, the slope of the line of best fit may not equal one, and intercept may differ from zero) while maintaining relative rank ordering of individuals. This, therefore, allows for potential effects such as habituation across tests or a gross change in behavioral patterns from early to late lactation.

To determine intertest consistency in behavioral metrics derived from the RCV tests the Intraclass Correlation Coefficient (ICC) was employed as a measure of repeatability (Lessells and Boag 1987, Bell *et al*. 2009). Repeatability is the "degree to which variation within individuals contributes to total variation in a population" (Boake 1989), and ICC is commonly used to measure the consistency of a particular behavior through time (Bell *et al*. 2009). Statistical analyses were performed using R version 2.12.0 (R Development Core Team 2010). We used ICC2 in the R package *psych* (Revelle 2010) which is a single measure two-way random effects model (Case 2 in Shrout and Fleiss 1979), therefore, both individual and sampling intervals are considered as random effects. For all ICCs shown $n_0 = 2$ (Bell *et al*. 2009).

Results

Remote Control Vehicle Performance

Overall the RCV performed extremely well on the terrain encountered on North Rona. The RCV had sufficient ground clearance, axle articulation, torque and power to climb over tussocky terrain (Fig. 2, see also supplementary video footage), and was robust enough to cope with occasional tumbles into hollows and pools of water and remained working even though it was exposed to wet and salty conditions in the field over an extended period. The RCV had adequate acceleration and speed to escape seals if necessary. Battery power was sufficient for at least seven tests on different females over various terrains, which often included climbing steep hills of up to 40° inclination on wet grass (Fig. 2). The major limitations of this prototype RCV were (1) the lack of a remotely controlled directional on board video with live streaming of video to the operator, which would have assisted in positioning of the RCV with respect to the target seal, and allow the camera angle to be adjusted to account for shifts in position of the target seal during tests; (2) the separate controls for the sound stimulus (as opposed to integrating the sound control mechanism within the RCVs own transmitter–receiver system) which proved to be the main restriction on the distance between operator and target seal (see Supporting Information); and (3) the noise of the electric motors which, although very quiet (approximately 55dB @ 1 m) compared to a petrol powered alternative, potentially provided an additional sound

Figure 2. Photograph illustrating the terrain negotiated by the RCV on North Rona, and the dispersion patterns of breeding seals.

stimulus on approaching the target seal. However, any effects from this additional noise were common across all test subjects, and were limited by providing the 5 min acclimation period.

Behavioral Responses—Females

All first tests were performed 4 d postpartum, however, due to weather conditions and other fieldwork commitments, intertest intervals for females varied. Of the 20 females tested twice, 12 had tests that were 10 d apart. Of the remaining eight females, four had tests that were 13 d apart, one female had tests separated by 7 d, and the remaining three females had tests only 4 d apart. However, the time between the first and second tests had no effect upon the degree of variation in individual responses to the two tests, either in terms of overall consistency (adjusted $r^2 = -0.04$, $F_{1,18} = 0.27$, $P = 0.61$) or the degree of deviation from absolute agreement (adjusted $r^2 = -0.05$, $F_{1,18} = 0.09$, $P = 0.77$). Similarly, the order in which individuals were tested during the breeding season had no effect on the number of pup checks performed either in the first (Spearman's rank correlation: $r = -0.12$, $n = 20$, $P = 0.60$) or the second test (Spearman's rank correlation: $r = 0.08$, $n = 20$, $P = 0.75$).

Of the 46 tests performed on the 26 different females, only one female retreated beyond their pup's location upon approach of the RCV. This test was abandoned immediately and shortly afterward the mother returned to her pup. The remaining seals stayed with their pups, typically shifting their location so that they were between their pup and the RCV. No females abandoned their pups, and with the exception of the aforementioned female that retreated none showed unusual behaviors during the tests. Females did, however, vary considerably in their responses to the RCV

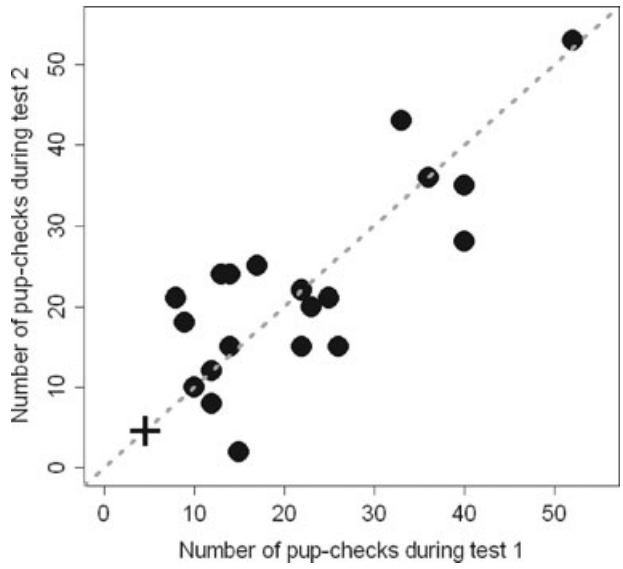

Figure 3. Intertest consistency in number of pup checks performed by postpartum female gray seals on North Rona in response to the RCV test (sound stimulus). Dashed line represents 1:1 line. + indicates mean baseline number of pup checks performed by females out with the test situation.

from almost completely ignoring the presence of the RCV and the sound stimulus to moderate threat displays (open mouth threats). Two females closely investigated the RCV by sniffing and pushing it with their muzzles. No females physically attacked the RCV. Examples of the range of behavioral responses by females are provided in the supplementary video footage.

Analysis of video footage for the number of pup checks performed during the test periods for females tested on two occasions (early and late lactation) revealed a very high and significant degree of repeatability (Fig. 3, ICC = 0.80, 95% CI = 0.56–0.92, $F_{19,19} = 8.6$, $P < 0.001$). Therefore, some females consistently performed pup checks at high rates in response to the test, whilst others consistently performed few pup checks. All females apart from one female in her second test (late lactation) performed more pup checks over the course of the test than would be predicted from baseline pup checking rates (Fig. 3). The mean baseline pup checking rate from the video focal samples of 11 mothers was 0.42/min (SE = 0.068/min), giving estimates of 4.67 ± 0.75 pup checks over an 11 min period (equivalent to the duration of the RCV test). By contrast, the number of pup checks performed by females in response to the RCV test ranged from two to 52 (Fig. 3).

Behavioral Responses—Males

Males varied considerably in their response to the approaching RCV. The proximity at which individual males became alert to the approaching RCV varied from one to six adult body lengths (one body length ≈ 2 m). Males responded by moving position either away from or towards the RCV at distances of 0.5 to six body lengths from the

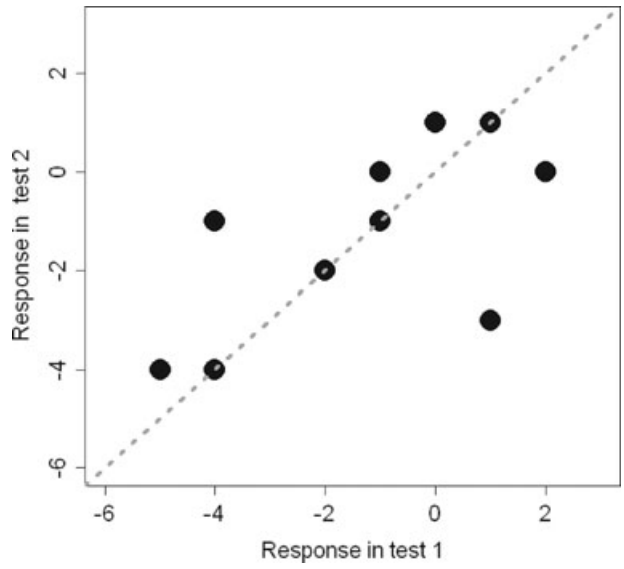

Figure 4. Intertest consistency in response of male gray seals to the approach of the RCV. Dashed line represents 1:1 line.

approaching RCV. Some males locomoted rapidly away from the RCV, coming to a halt elsewhere within their respective home ranges. Other males remained stationary, showing little active inspection of the RCV, but allowing the RCV to approach to within one body length, while other males were more inquisitive and approached the RCV, sniffing and nosing the RCV. Some males approached the RCV and threatened it (open mouth threats), but no males physically attacked the RCV. Examples of the range of male responses can be seen in the supplementary video footage.

The 12 males who were tested twice during their stay on the colony showed a significant repeatability of response to the RCV (Fig. 4, ICC = 0.68, 95% CI = 0.19–0.90, $F_{11,11} = 5.0$, $P = 0.007$). Six of these males had repeat tests 4 d apart, one at 6 d, two at 7 d, and three males at 10 d separating tests. However, the time between the first and second tests had no effect upon the degree of variation in individual responses to the two tests, either in terms of overall consistency (adjusted $r^2 = -0.04$, $F_{1,10} = 0.57$, $P = 0.47$) or the degree of deviation from absolute agreement (adjusted $r^2 = 0.01$, $F_{1,10} = 1.17$, $P = 0.31$).

Discussion

Although a prototype, the RCV tested here proved to be very successful in delivering a reasonably standardized in-field test of behavioral types for female gray seals (less so with males) and yielded data clearly showing strong individual consistencies in behavioral responses to repeated tests over time. Although it would be preferable to standardize intertest interval for all seals tested, the results presented here show clear consistency in individual responses to the test across time points with no discernible effect of variation in intertest period, therefore, making the test

amenable to the unpredictable nature of field conditions. It is particularly noticeable that both female and male patterns of repeatability fit closely to the 1:1 line, indicating not only consistent individual differences in behavior, but also limited plasticity in the response of individuals to the two tests. The test worked particularly well with females because they tended to stay with their pups, which are relatively immobile. Therefore, in all tests on females (except for one female) the RCV could be positioned within two body lengths of the target seal and the full set of sound stimuli performed. Males, however, varied considerably in their response to the approaching RCV, making test conditions less standardized. Unlike the females, males have no pup to protect, and, therefore, upon approach of the RCV, many would retreat to another part of their home range. In addition the metric used for males was based on a qualitative judgment of the male's response by the observer. However, despite this, repeatable responses were evident. Most importantly, the tests succeeded in eliciting measurable responses from seals without causing harmful disturbance to the target seals or their neighbors. Although some males moved away from the RCV, movements were confined to within their home ranges, and no males were displaced from their home ranges due to the use of the RCV.

There is ongoing debate about what consistent individual differences in behavior or behavioral types represent (Sih *et al*. 2004*a*, *b*; Dingemanse and Réale 2005; Bell 2007*a*, *b*; Réale *et al*. 2007; Sih and Bell 2008; Bell *et al*. 2009; Biro and Stamps 2010); particularly whether they are adaptive behavioral phenotypes or the product of mechanistic constraints (physiological, morphological, and/or genetic linkages). Why female gray seals express individually consistent patterns of pup checking is also unknown. It is likely that the levels of pup checking exhibited by females in response to the test indicate differing levels of maternal attentiveness towards their pups (Fairbanks 1996, Albers *et al*. 1999, Hill *et al*. 2007). However, it might be expected that females should be able to modulate such behavior in accordance with requirements, but the results shown here suggest that this is not the case, and that some females consistently perform high rates of pup checking, while others consistently perform low levels, even in response to the same standardized stimulus. These findings highlight the need to understand more fully the meaning (to the mother) of pup checks along with other behaviors and to ascertain the fitness consequences of differing levels of maternal attentiveness. If either high or low levels of maternal social attentiveness contribute to greater fitness, one would be forced to ask why selection has not favored a single optimum level of pup checking, or indeed a degree of plasticity in pup checking, which, according to these data, seems to be absent. Therefore, it will be necessary to conduct further detailed analyses of the social contexts in which pup checks occur in nontest situations in order to state more confidently what these consistent differences in behavior mean. Although pups generally showed little or no interest in the RCV, or response to the "wolf" calls, detailed analyses of the interactions of mothers and their pups will also be necessary for a full interpretation of pup checking behavior exhibited during the tests.

The behavioral metric used for assessing male responses to the RCV is not a continuous variable, and, therefore, ICC may not be the most appropriate statistical tool in this case (although the observed relationship is quite robust, and an alternative approach of applying a Spearman's rank correlation shows a significant relationship; $r = 0.66$, $n = 12$, $P = 0.018$). Furthermore, although male responses do show consistency, individual responses may be dictated by their mating strategy and social status. Male strategies range from subordinate transients to resident, tenured,

typically dominant, males (Twiss *et al*. 1998, 2006*a*). All males tested here were tenured males, though there was variation in the location and size of male home ranges and the number of females within those home ranges (SDT, personal observations). Males occupying central locations tend to have more females within their home ranges (Twiss *et al*. 1998, 2006*a*). Males with more peripheral locations are generally associated with only one or two females. These peripheral males may adopt a mate guarding strategy, and be more motivated to stand their ground in response to perceived threats. Males with more females in their home range may be less willing to defend individual females and have the option of moving elsewhere within their home range. Anecdotal observations during the RCV tests seemed to suggest such a possibility, with the males that occupied home ranges with more females tending to be those that moved away from the RCV most rapidly (SDT, personal observations). Disentangling the links between behavioral response to the test and male strategies will require repeated testing of individuals over successive years to identify if males who change strategy over years remain consistent in their response to the RCV.

The RCV described here has clear potential for use in studies of breeding gray seals, however, can this, or a similar method be used in other marine mammal study systems? There are key features of gray seal breeding colonies that make them a tractable study system for *in situ* studies of behavioral types using techniques such as the RCV described here. First, individuals are identifiable, and beneficially this can be done using "hands-off" photo-ID techniques, therefore, avoiding the necessity to handle animals. Second, breeding females tend to remain with their pups throughout lactation, enabling close approach of the RCV to the mother, and permitting repeat tests within seasons. Third, fine spatial scale inter-annual site fidelity of females (median interannual distance moved from previous pupping sites = 55 m; Pomeroy *et al*. 1994) permits interannual repeat tests of known individuals to examine longer term repeatability of behavioral responses. Males show similar interannual site fidelity (median interannual distance between territory centers = 53 m; Twiss *et al*. 1994), but only approximately 33% of males return to the colony in successive seasons, with the majority of males being present for three or fewer successive seasons (Twiss *et al*. 1998). To perform such tests in other marine mammal species requires these key features of identifiable individuals, approachability and the opportunity to retest the same individuals at a later time. It must also be noted that gray seal breeding colonies are at a relatively low density compared to some other pinnipeds (Pomeroy *et al*. 1994, 2001; Twiss *et al*. 2000). This provides adequate room for maneuvering the RCV between seals. Furthermore, the terrain on North Rona although rough was navigable by this design of RCV. Where seals breed for example on beaches comprised of large irregular boulders and/or in high densities with little space between neighbors application of an identical RCV would be potentially difficult and alternative designs must be considered, such as tracked vehicles or even airborne vehicles. Though the current design is for terrestrial use, the general principle of a remotely operated vehicle to deliver standardized behavioral tests is one that is not solely restricted to terrestrial environs. Similar remotely controlled devices could potentially be designed for approaching (or attracting) individuals at sea.

Data from these tests together with repeated testing on the same and other gray seals over successive breeding seasons will be useful in analyses of variation in individual success. Previous studies have shown that there is considerable variation in individual reproductive success in female gray seals, with approximately 57% of breeding females producing 75% of the pups that survive to weaning, yet attempts to explain this variation using energetic, morphometric and age data account for

only approximately 30% of the observed variation in female success (Pomeroy *et al*. 1999). It will be instructive to examine how individual behavioral types relate to variation in fitness once a sufficiently large sample size is collected.

Most studies of behavioral types and personality use laboratory based tests (Réale *et al*. 2007, Smith and Blumstein 2008, Bell *et al*. 2009). It may be argued that laboratory tests are desirable as one is more able to standardize test conditions. There is however, limited evidence at present that behavioral types expressed in captivity reflect actual behavioral patterns in the wild (Herborn *et al*. 2010), and links between personality in the wild and captivity may well be species specific (Minderman *et al*. 2009, Herborn *et al*. 2010). Conversely, behavioral patterns shown in the wild may be absent in captivity (Wilson *et al*. 1993). More studies of consistent individual differences in natural populations and their relationships with other behavioral and ecological measures (*e.g*., social interactions, habitat use) and measures of fitness, are required to gain a full understanding of the ecological and evolutionary relevance of behavioral types (Smith and Blumstein 2008, Bell *et al*. 2009). Twiss and Franklin (2010) used a purely observational approach to provide evidence of high levels of interannual consistency in wild male gray seal behavior patterns that were unrelated to age, size, indices of energy expenditure, patterns of colony attendance and utilization, levels of sexual or aggressive behavior or dominance status. However, unless one is also able to collect fine spatial and temporal resolution data on the local environment that individuals experience it is difficult to state that observed behavioral consistencies are not simply a product of individuals experiencing the same stimuli at the time points observed. The method presented here provides a more robust and standardized field-experimental test for behavioral consistencies.

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Supporting Information

The following supporting information is available for this article online:
Video 1: Female responses.
Video 2: Male responses.

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Short Note

Observations from Video Footage of Red Fox (*Vulpes vulpes*) Activity Within a Grey Seal (*Halichoerus grypus*) Breeding Colony on the UK Mainland

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Pinnipeds are highly adapted to the marine environment, yet they are constrained to give birth and raise their pups on land or ice (Bartholomew, 1970). As a result, terrestrial predators present a major threat to breeding pinnipeds; this is particularly true for newborn pups, which are especially vulnerable (Kovacs, 1987). For that reason, it is generally accepted that avoidance of terrestrial predators is one of the main selective pressures that lead pinnipeds to use remote and uninhabited locations, such as offshore islands, as breeding sites (Bartholomew, 1970; Hindell, 2009). There are numerous reports of terrestrial predators regularly scavenging or predating on ice breeding pinnipeds in Arctic regions where the seals do not have access to island sites (Andriashek et al., 1985; Derocher et al., 2002; Roth, 2002). Such predation pressures can have a considerable impact upon breeding success; for example, studies from northern Canada have reported that polar bears (*Ursus maritimus*) take up to 44% of the estimated annual pup production of ringed seals (*Phoca hispida*; Hammill & Smith, 1991). Arctic foxes (*Alopex lagopus*) have also been reported to predate on ringed seals, taking an average of 26.1% of the estimated pup production over a 3-y period (Smith, 1976). Where pinnipeds form mainland breeding colonies, terrestrial predators can also impact pup survival; for example, brown hyenas (*Parahyaena brunnea*) are known to take up to 9.6% of Cape fur seal (*Arctocephalus pusillus pusillus*) pups on mainland breeding colonies in Namibia, Africa (Wiesel, 2010).

Of the two pinniped species in the UK, harbour seals (*Phoca vitulina*) minimise the risk of terrestrial predation by forming breeding colonies on sheltered inter-tidal sites where soon after parturition, the mother and pup will enter the sea (Summers et al., 1980; Cordes et al., 2011). Grey seals (*Halichoerus grypus*) typically breed on offshore islands or inaccessible sea-caves where terrestrial predators do not occur. Unlike harbour seals, grey seal pups remain on land from birth, and mothers typically remain with the pup throughout the period of lactation (Pomeroy et al., 1999). After weaning, the pups can remain on the colony unattended for up to several weeks (Fedak & Anderson, 1982). Historically, potential terrestrial predators of UK grey seals included wolves and bears, but more recently, their major terrestrial predators have been humans, with grey seal culls occurring from 1958 to 1985 (Lambert, 2002). With changes in legislation and public opinion over the last three or four decades, which consequently resulted in the end of the grey seal culls (Lambert, 2002), there appears to have been a corresponding increase in the number of grey seal breeding colonies forming on the UK mainland. As a consequence, grey seals at these sites may have to contend with threats from terrestrial predators. The largest of these mainland breeding colonies is at Donna Nook, Lincolnshire, where pup production increased from 618 in 2000 to 1,417 in 2010. It is from Donna Nook that we present evidence of red fox (*Vulpes vulpes*) activity within a grey seal breeding colony and discuss the implications of these observations.

Donna Nook (53° 28' N, 0° 9' E) is located on the Lincolnshire coast, near North Somercotes, UK, where the Humber Estuary opens to the North Sea. Annually, between November and December, the Donna Nook National Nature Reserve is host to a large breeding colony of grey seals that gathers on the sand flats far inshore close to publicly accessible areas patrolled by Lincolnshire Wildlife Trust (LWT) wardens. The grey seals also use areas adjacent to the Defence Training Estate Donna Nook Air Weapons Range, where public access is

restricted. It was within this area of the colony that this observational study was conducted.

Nighttime video footage was recorded using a custom-made weatherproof camera constructed by Astra Communications Ltd (Bristol, UK). The specifications of the camera were 540TV colour/monochrome, 9 to 22 mm auto-iris lens with a minimum illumination of 0 Lux. A weatherproof infrared (IR) lamp was used to increase the area of illumination; the lamp had an output of 850 nM IR with a range of up to 40 m and an IR spread of 30°. The footage was recorded to a 32 GB SD flash memory card via a Vista MiniD400. The camera, lamp, and recording equipment were powered using two 12-v car batteries. Video footage was collected continuously between 1600 to 0800 h over three nights—25 November and 7 and 8 December 2010—resulting in a total of 2,880 min of footage. A small area (approximately 10 m × 8 m) at the periphery of the main breeding colony was filmed. The size of the area under observation was limited by the field-of-view of the camera and the IR spread.

There were a total of 10 occurrences of red fox activity recorded (which may or may not have been the same individual) on two of the three nights (25 November and 8 December 2010; Table 1). An occurrence was defined as a fox entering and leaving the frame for longer than 60 s. If the fox re-entered the frame within this time, it was assumed to be the same fox, and it was regarded as the same occurrence.

There was no direct interaction between the red fox and grey seal(s) in any of the 10 occurrences; however, on three occurrences, as a fox passed through the breeding colony, adult seals clearly displayed a head-up "alert" behaviour (Twiss et al., 2000). This behaviour was only observed on 25 November 2010 (Table 1; Figure 1a). On the same date, there were two occurrences in which a fox stopped at the same location and took an interest in something on the ground. The fox appeared to have its muzzle near to, if not on, the ground during both occurrences (Table 1; Figure 1b). On the morning of 26 November, several carrion crows (*Corvus corone*) were filmed (using the same camera) as they gathered at the same location that the fox stopped at the night before. The crows can be seen pecking and lifting at what looks to be carrion, perhaps placenta (Figure 1c), although the footage is not clear enough to state this with any confidence. Because the video was analysed after the field season ended, it was not possible to investigate the site to determine what might have been of interest to the fox and crows.

The red fox has a renowned generalist diet and is known to forage opportunistically (Leckie et al., 1998; Webbon et al., 2006). Although we acknowledge that we do not present clear evidence of scavenging or predation by red foxes, it is likely that the foxes were foraging within the breeding colony and could have been scavenging on seal placentae (approximately 3 kg each) or on dead or starving pups. The LWT wardens have found evidence of placentae that had been dragged from the sand flats to the sand dunes, and they have also found the remains of dead pups that had been fed upon—all of these findings were assumed to be the result of foxes (Lidstone-Scott, pers. obs.; most recently recorded on 24 November 2010).

It is well-documented that red fox populations suffer higher mortality rates during the winter, which occurs immediately prior to the onset of their breeding period (Heydon et al., 2000; Webbon et al., 2006). Consequently, food availability at this time of year is likely to have an important influence on pre-breeding numbers. Although the diet of red foxes in the UK over the winter period is diverse, there is no evidence that red foxes feed on grey seals (Leckie et al., 1998;

Table 1. Summary of video footage of red fox activity within the grey seal breeding colony at Donna Nook; seal disturbance is defined as a head-up "alert" behaviour by one or more seals, occurring either within 10 s prior to the fox entering the area under observation, during the time the fox is present within the area under observation, or up to 10 s after the fox left the area under observation.

Date	Seal disturbance	Time entered frame	Occurrence number
25 Nov 2010	Yes	2114 h	1
25 Nov 2010	No	2134 h	2
25 Nov 2010	Yes	2140 h	3^
25 Nov 2010	No	2145 h	4
25 Nov 2010	Yes*	2219 h	5^
25 Nov 2010	Yes*	2253 h	6
25 Nov 2010	No	2255 h	7
26 Nov 2010	No	0420 h	8
9 Dec 2010	No	0134 h	9
9 Dec 2010	No	0445 h	10

*A female with a pup in frame performs an "alert" behaviour in the direction of her pup

^The fox has its muzzle close to, if not on, the ground

Figure 1. Screen shots of the video footage showing (a) a fox passing through the colony with a pup and its mother in the centre of the frame and a mother at the lower right of the frame; both mothers are performing an "alert" behaviour; (b) a fox with its muzzle near to, if not on the ground; the eyes of the fox assist in identifying the position of the muzzle; and (c) a carrion crow pecking at what is assumed to be carrion (perhaps placenta) in the same area that the red fox was the night before. The time date stamp (YYYY-MM-DD, HH:MM:SS) is shown in the top left corner of each screen shot. Contact the corresponding author for access to the video footage.

Webbon et al., 2006). However, the most comprehensive of these studies collected scat samples (which were used to identify hard tissue) between February and March 1999 and 2000 (Webbon et al., 2006), which is shortly after the grey seal breeding season at Donna Nook. Therefore, it is unsurprising that the authors found no evidence of red foxes feeding on grey seals. We suggest that in addition to extracting hard tissues from scat samples, PCR amplification of mitochondrial DNA segments from DNA extracted from the fox scat also should be used in order to identify suspected prey species in the absence of hard tissues (Deagle et al., 2005; Hofreiter et al., 2010). This could be done for fox scat samples collected at Donna Nook during the grey seal breeding season to ascertain if red foxes are feeding on placentae or seal pups, and if so, to what extent.

The largest contributing factors to pup mortality rates on island breeding colonies in the UK are starvation and infection, often as a consequence of the mother-pup bond not forming or being broken (Anderson et al., 1979; Redman et al., 2001). This bond is established immediately after parturition, but disturbances during this period can hinder bond formation. Although disturbance to grey seals was not recorded during every occurrence of red fox activity (Table 1), it is important to note that of the few mothers that were recorded, all had pups that were approaching weaning age (approximately 12 to 16 d old). Therefore, it was not possible to assess whether or not the activity of foxes in any way affected the mother-pup bond formation.

Previous studies have shown that interspecific disturbance to mothers and pups by lesser and greater black back gulls (*Larus fuscus* and *L. marinus*, respectively) is common on island breeding colonies where the gulls often scavenge for the placenta immediately after parturition (Twiss et al., 2003). It has been suggested that females that give birth on the periphery of a colony are possibly more susceptible to disturbance by gulls because of lower densities of seals in these colony regions (Redman et al., 2001; Twiss et al., 2003). The video evidence of red fox activity discussed in this paper was collected at the periphery of a colony; therefore, the same also may be true in regards to scavenging by foxes as it is for gulls.

A further consideration is that the distribution patterns of adult grey seals may also influence the foraging opportunities for red foxes. Previous studies show that fine-scale topography has a major influence on seal distribution on breeding colonies (Twiss et al., 2001), with heterogeneous topography at island sites leading to aggregated distributions of females (Twiss et al., 2000, 2001). Conversely, the topography of Donna Nook is more homogenous, comprising large expanses of relatively flat sand, which appears to promote a less clumped, more uniform spatial distribution of seals. A lower density of seals may allow foxes to move more easily within the colony at Donna Nook, again providing opportunities for scavenging; however, the

Table 2. Summary of the range and average pup mortality figures from three well-established island grey seal breeding colonies and Donna Nook

Location	Year(s)	Range of pup mortality	Average pup mortality	Reference
Farne Islands	1956-1962	10.5-17.9%	14.9%	Coulson & Hickling, 1964
Isle of May	1986	--	12.5%	Baker & Baker, 1988
North Rona	1959-1968	14.5-25.0%	19.2%	Boyd & Campbell, 1971
North Rona	1972	--	30.0%*^	Summers et al., 1975
North Rona	1997-1998	14.4-14.6%	14.5%*	Twiss et al., 2003
Donna Nook	2001-2010	5.2-11.5%	9.0%	Lidstone-Scott, unpub. data

*Data not from the entire breeding colony
^Pup mortality rate is an estimate

average pup mortality for the entire Donna Nook breeding colony between 2001 and 2010 was 9%, which is comparatively lower than island breeding colonies which have ranged between 12.5 and 30% (Table 2). This raises the question of how female seals respond to foxes. If mothers are more attentive of their pups or maintain closer proximity to their pups compared to island sites that are free from potential terrestrial predators, then their behaviour may help account for the lower mortality rates in pups at Donna Nook. Disentangling this explanation from the potential effects of lower seal density would require a detailed study, although Twiss et al. (2003) showed no direct link between local adult density and likelihood of pup death.

The extent to which red fox activity impacts upon grey seals during the breeding season is not clear from the observations presented herein; however, we do consider it to be highly improbable that the occurrence of foxes in this area was by random chance alone. Given that red foxes often occur in high densities (Heydon et al., 2000; Webbon et al., 2004) coupled with the small size of the area under observation, it is more than likely that fox activity is a regular occurrence throughout the breeding colony. Consequently, we suggest that the interactions between red foxes and grey seals at Donna Nook should be investigated further in order to gain a greater understanding of whether or not the presence of red foxes is affecting mother-pup behaviour, colonisation patterns, and pup mortality rates.

A final intriguing implication of the video footage discussed herein relates to the possible origin of disease outbreaks in pinnipeds. Grey seals and harbour seals have experienced several outbreaks of phocine distemper virus (PDV) since it was recognised in 1988 (Cornwell et al., 1992; Hall et al., 1992). PDV is a morbillivirus closely related to the canine distemper virus. There is much debate over (1) where PDV originated and (2) how the outbreaks began. We do not suggest that the red foxes at Donna Nook were responsible for past PDV epidemics (especially as these occurred prior to the major expansion of the Donna Nook seal colony, with 709 pups produced during the 2002 epidemic, which is approximately half of the current pup production rate; Lidstone-Scott, unpub. data). Still, the observations presented herein illustrate the potential for close proximity of canids and pinnipeds at mainland breeding sites and, therefore, the potential for cross-species zoonoses, including rabies.

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Fred was a close friend to many of us and we had the pleasure of flying with him for many hundreds of hours on marine mammals surveys, as well as working with him on the ground. Among other things, we remember him for his keen observational abilities, his fathomless curiosity, vivacity, and wonderful sense of humor.

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